

# The Marine Benthic Algal Flora of Puerto Rico, II. Chlorophyta and Prasinodermatophyta

*David L. Ballantine, James N. Norris,  
and Hector Ruiz*



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## ABSTRACT

Ballantine, David L., James N. Norris, and Hector Ruiz. *The Marine Benthic Algal Flora of Puerto Rico, II. Chlorophyta and Prasinodermatophyta*. Smithsonian Contributions to Botany, number 117, x + 164 pages, 116 figures, 2023. — This treatment is a taxonomic study of the benthic species of Chlorophyta known from Puerto Rico, Caribbean Sea. In all, 2 classes, 8 orders, 25 families, 50 genera, and 150 species occur in the benthic marine communities in Puerto Rico. Along with date, place, and author(s) of valid publication for all genera, species, and infraspecific taxa, type locality information and descriptive accounts of vegetative morphological and reproductive anatomy are provided. Distribution of each species is given, and where relevant, comments on their habitat and taxonomic and nomenclature status are discussed. A key to the genera and keys to species within genera are included. Either an in situ image or an illustration accompanies most species. Two varieties each of *Bryopsis pennata* and *Caulerpa cupressoides*; one variety each of *Caulerpa chemnitzia*, *C. racemosa*, and *Udotea occidentalis*; and a single forma each of *Halimeda opuntia* and *Udotea cyathiformis* are reported for Puerto Rico for the first time. *Avrainvillea mazei*, *Anadyomene howei*, *A. rhizoidifera*, and *Caulerpa parvifolia* are also reported as new geographic records for Puerto Rico. A new section of *Ulva*, sect. *Chaetomorphoides* J. N. Norris et D. L. Ballant., is established. Descriptions of one new combination, *Halimeda acerifolia* (D. L. Ballant.) D. L. Ballant. et J. N. Norris, and two new forma, *Udotea cyathiformis* f. *mesophotica* D. L. Ballant, H. Ruiz, et J. N. Norris and *U. occidentalis* f. *radiata* D. L. Ballant. et J. N. Norris, are included.

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Cover images, from left: *Halimeda discoidea* (Figure 44), *Caulerpa racemosa* (Figure 17A), *Udotea flabellum* (Figure 74B).

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David L. Ballantine,<sup>1\*</sup> James N. Norris,<sup>1</sup> and Hector Ruiz<sup>2</sup>

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## INTRODUCTION

This work is the second volume of the marine algal flora of Puerto Rico (Figure 1), covering Chlorophyta. The first volume, *The Marine Benthic Algal Flora of Puerto Rico, I. Ochrophyta: Phaeophyceae, Pelagophyceae, and Xanthophyceae* (Ballantine et al. 2021), covered 77 species of Puerto Rican brown algae, including one new species, an account of habitat types for the island, and a history of phycology in Puerto Rico. Collector and herbarium abbreviations used in text are defined as follows:

DLB	David L. Ballantine
D&ML	Diane and Mark Littler
DUKE	Duke University
LD	Herbarium Agardh, Lund University
LRA	Luis Raul Almodóvar
MAH	Marshall A. Howe
MDP	Manuel Díaz-Piferrer
MEL	Royal Botanic Gardens Victoria
MSM	University of Puerto Rico
PC	Muséum National d'Histoire Naturelle
NY	New York Botanical Garden
SAE	Sylvia A. Earle
US Alg. Coll.	Algal Collection, U.S. National Herbarium

## ATTRIBUTIONS

Authority names of taxa are abbreviated according to Brummitt and Powell (1992), and herbarium abbreviations follow Thiers (2020). Unless otherwise indicated, in situ photos, laboratory-based photographs, and herbarium specimen scans are of algae from Puerto Rico. We have followed the taxonomic arrangement of Wynne (2017). Within orders, subordinate taxa are alphabetically arranged. Type and type localities are from original publications where possible. Species distributions are mostly culled from Taylor (1960), Guiry and Guiry (2022), and original literature. Within distributions, we use, for convenience, “Netherlands Antilles” for records pertaining to Aruba, Bonaire, and Curaçao. As a political entity, the Netherlands Antilles was officially dissolved in 2010.

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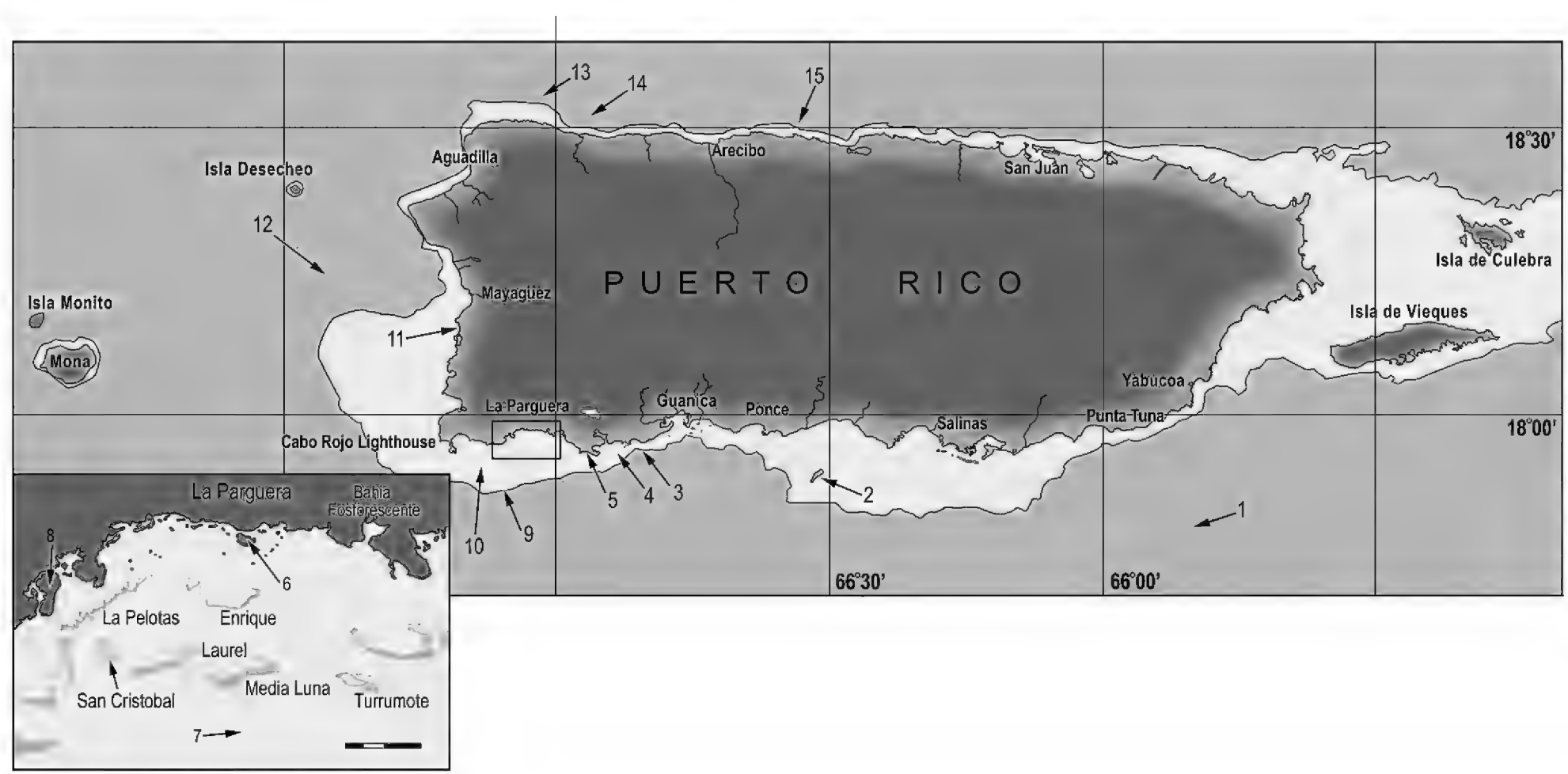


FIGURE 1. Map of Puerto Rico showing frequent collection sites. The depth contour surrounding the island represents a depth of 50 m. (1) Grappler Bank, (2) Caja de Muertos, (3) shelf edge off Salinas (off Guánica), (4) Punta Brea algal plain, (5) Ballena Bay, (6) Magueyes Island, (7) Media Luna algal plain, (8) Guayacán Island, (9) “Buoy,” (10) Margarita Reef algal plain, (11) Punta Arenas, (12) Bajo de Sico, (13) Isabella, (14) Guajataca, (15) Islote. The scale bar in the La Parguera inset = 2.0 km.

Keys and species accounts are only partially original, as much of the information herein has been assembled from a variety of sources. Portions of keys and taxa accounts are derived from original literature (cited with corresponding taxa) in addition to the compilations of Taylor (1960), Humm and Taylor (1961), Abbott and Hollenberg (1976), Schneider and Searles (1991), Brodie et al. (2007), Dawes and Mathieson (2008), Huisman (2015), and Guiry and Guiry (2022).

The works of Söderström (1963), Hoek (1963), Hoek and Chihara (2000), and, particularly, Hoek (1982) were used in determining species of *Cladophora* and preparing their descriptive accounts.

The following is an artificial key to genera of Chlorophyta of Puerto Rico. Users of the key should bear in mind that its use for algae not currently recognized for Puerto Rico may not necessarily result in keying to a correct genus.

KEY TO THE GREEN ALGAL GENERA OF PUERTO RICO

- 1. Thalli consisting of unicells, embedded in a gelatinous matrix ..... 2  
Thalli not as above ..... 3
- 2. Thalli globose, attached across the entire contacting surface ..... *Pseudotetraspora*  
Thalli peltate attached by haptera or thalli erect ..... *Verdigellas*
- 3. Plants coenocytic, not divided by cross walls ..... 32  
Plants not as above ..... 4
- 4. Plants of microscopic filaments united to form discs or microscopic erect or endophytic or endolithic filaments ..... 5  
Plants macroscopic ..... 8
- 5. Plants of microscopic prostrate discs; the discs may be composed of filaments ..... *Ulvella*  
Plants of microscopic endophytic or endolithic filaments ..... 6
- 6. Hairs present ..... *Phaeophila*  
Hairs absent ..... 7
- 7. Distinctive sporangia present ..... *Gomontia*  
Distinctive sporangia absent ..... *Acrochaete*

8. Plants composed of vesicular cells, few to many, multinucleate, attached by rhizoids or small vesiculate cells ..... 9  
Plants not as above ..... 11
9. Plants composed of distinctly vesicular cells ..... 10  
Plants of many laterally joined cells that form a solid or hollow parenchymatous structure ..... *Dictyosphaeria*
10. Plants with elongate vegetative cells, solitary or a few together, basally annular constrictions ..... *Boergesenia*  
Plants of few to many vegetative cells, lacking annular constrictions ..... *Valonia*
11. Plants composed of branched or unbranched uniseriate filaments; if a bladelike structure is present, it is netlike, not solid ..... 12  
Plants not filamentous, or if filamentous, the filaments either unite to form solid blades or tubes or are multiseriate at. . . least in part ..... 28
12. Filaments unbranched ..... 13  
Filaments branched ..... 14
13. Filament diameter less than 30  $\mu\text{m}$  ..... *Pseudorhizoclonium/Rhizoclonium*  
Filament diameter greater than 30  $\mu\text{m}$ , cells frequently thick walled ..... *Chaetomorpha*
14. Branches in distinct whorls, some of which may or may not become fused laterally ..... 15  
Plants not branched as above ..... 21
15. Branches fused laterally ..... 16  
Branches not fused laterally ..... 17
16. Mature disc less than 3 mm in diameter, corona inferior absent ..... *Parvocaulis*  
Mature disc more than 3 mm in diameter, corona inferior present ..... *Acetabularia*
17. Plants not calcified ..... 18  
Plants calcified ..... 20
18. Whorls of branchlets few; whorl branchlets rebranched in whorls ..... *Ernodesmis*  
Whorls of branchlets many along the same axial filament ..... 19
19. Whorls of branchlets closely set; sporangia single and terminal on the basal cell of each branchlet cluster ..... *Dasycladus*  
Whorls of branchlets distant; sporangia several per branchlet cluster ..... *Batophora*
20. Plants small, whorls of branchlets closely set, forming a continuous surface ..... *Neomeris*  
Plants larger, abundantly branched; with a segmented stalk; branch tips with tufts of filaments ..... *Cymopolia*
21. Distal branches uniting or anastomosing to form a net ..... 22  
Plants not branched as above ..... 25
22. Original cell constituting the greater part of a stalk, above which it differentiates into a bladelike structure composed. . . of oppositely branching filaments that anastomose to form a net ..... 23  
Original cell not forming a distinctive stalk ..... 24
23. Branches formed by nonsynchronous centripetal cross-wall growth ..... *Phyllodictyon*  
Cell division segregative ..... *Struvea*
24. Plants foliar, filaments closely branched in one plane ..... *Microdictyon*  
Plants not foliar, small to microscopic; filament branches joined by haptera at branchlet tips into a spongy mass ..... *Boodlea*
25. Plants with an elongate stalk of large annulate, somewhat calcified cells bearing a terminal noncalcified tuft of filaments ..... *Chamaedoris*  
Plants not as above, filamentous ..... 26
26. Microscopic thalli, irregularly branched with bulbous inflations ..... *Bolbocoleon*  
Macroscopic thalli without bulbous inflations ..... 27
27. Septa formed at base of branches ..... *Cladophora/Willeella*  
Septa either absent (in young branches) or produced distal to the base of the branch ..... *Cladophoropsis*
28. Plants forming bushy tufts above a stalk that becomes pluriseriate with age ..... *Siphonocladus*  
Plants forming either a solid blade or tube ..... 29
29. Plants forming a simple tube, tube walls when viewed in section, 1 cell thick ..... *Ulva* (in part)  
Plants forming a flat blade ..... 30
30. Blades 1 cell thick, cells of the blade of different sizes, larger cells forming veins ..... *Anadyomene*  
Blades 1–2 cells thick, cells of the blade of similar sizes ..... 31
31. Thalli 1 cell thick in section ..... *Gayralia*  
Thalli membranous and 2 cells thick in section ..... *Ulva* (in part)

32. Plants microscopic, endolithic .....	<i>Ostreobium</i>
Plants macroscopic .....	33
33. Plants filamentous, the filaments not united to form larger distinctive structures .....	34
Plants not filamentous, or if filamentous, the filaments united to form larger distinctive structures .....	41
34. Plants forming a monostromatic or partially distromatic blade above a monosiphonous stipe .....	35
Plants not as above .....	36
35. Blade filaments conjoined by lateral processes or by filaments running perpendicular to the blade's parallel filaments ...	
.....	<i>Rhipiliopsis</i>
Blade filaments loose, or if filaments are adhering, not adhering by lateral processes .....	<i>Rhipidosiphon</i>
36. Plants forming short branchlets in more or less regular lateral series .....	37
Plants not as above .....	39
37. Branchlets bearing large gametangia near base .....	38
Branchlets without distinctive gametangia .....	<i>Bryopsis</i>
38. Chloroplasts lack pyrenoids; gametangia separated from its bearing branch by a plug .....	<i>Pseudobryopsis</i>
Chloroplasts possess pyrenoids; gametangia without plugs .....	<i>Trichosolen</i>
39. Filaments ditrichotomously branched, branchlets constricted sharply at their base .....	<i>Boodleopsis</i>
Filaments not constricted above dichotomies .....	40
40. Plants staining dark blue with I2KI .....	<i>Derbesia</i>
Plants not staining dark blue with I2KI .....	<i>Vaucheria</i>
41. Plants more or less calcified .....	47
Plants not calcified .....	42
42. Trabeculae present, plants consist of a rhizome, rhizoids, and erect blades or branches (in a few species, these are not obviously differentiated) .....	<i>Caulerpa</i>
Plants not as above .....	43
43. Plants with a stipe, the stipes are clearly differentiated from the rest of the plant .....	45
Plants not stalked, upper and lower portions not differentiated .....	44
44. Thallus filaments producing utricles peripherally .....	<i>Codium</i>
Thallus filaments not producing utricles .....	<i>Avrainvillea</i> (in part)
45. Foliar portion with distinctive (repeatedly divaricately dichotomous) cortical filaments .....	<i>Cladocephalus</i>
Blades without differentiation of cortex .....	46
46. Blades or foliar lobes soft, thick or thin, blade filaments without specialized structures .....	<i>Avrainvillea</i> (in part)
Blades thin, filaments with adventitious diverticula .....	<i>Rhipilia</i>
47. Plants distinctly segmented .....	<i>Halimeda</i>
Plants not distinctly segmented .....	48
48. Foliar portion consisting of a tuft of unconsolidated filaments .....	<i>Penicillus</i>
Foliar portion of consolidated filaments held together to make up 1 or more blades .....	49
49. Upper portion a flat blade or cup-shaped expansion .....	<i>Udotea</i>
Upper portion not in one plane, composed of an aggregation of small overlapping flat blades .....	<i>Rhipocephalus</i>

# The Chlorophyta and Prasinodermatophyta Species of Puerto Rico

---

## CHLOROPHYTA REICHENBACH

## CHLOROPHYTINA CAVAL.-SM.

## CHLOROPHYCEAE WILLE

## CHLAMYDOMONADALES F. E. FRITSCH

## PALMELLOPSIDACEAE KORSHIKOV

## *Pseudotetraspora* Wille

*Pseudotetraspora* Wille 1906: 20.

Thalli consist of gelatinous colonies, irregularly subspherical in shape, that can become compressed, contorted, or wrinkled. Minute coccoid cells occur in groups of 2–4 and are more concentrated peripherally than within the matrix. Cells are uninucleate, with a chloroplast (chromatophore) and a central pyrenoid. There are three species of *Pseudotetraspora* currently recognized, one of which is found in Puerto Rico.

## *Pseudotetraspora marina* Wille

### FIGURE 2

*Pseudotetraspora marina* Wille 1906: 20, pl. 1, figs. 32–36.

*Heterotypic Synonym: Pseudotetraspora antillarum* M. Howe 1920: 597.

*Puerto Rican Records:* As *Pseudotetraspora marina*: Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Mexico, North America, Bahamas, Puerto Rico, Sargasso Sea.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Steinviksholm, Drontheimsfjord, Norway.

*Pseudotetraspora marina* is the generitype species. Thalli consist of gelatinous masses that are subglobose to flattened, 2.0–20 mm diameter (diam). Uninucleate cells are coccoid to oval, 3.0–7.0  $\mu\text{m}$  diam, and possess a single chloroplast with a central pyrenoid. Cells usually occur in clusters of 4. They are scattered within the gelatinous matrix, sometimes more concentrated near the periphery. Algae are yellowish brown in color.

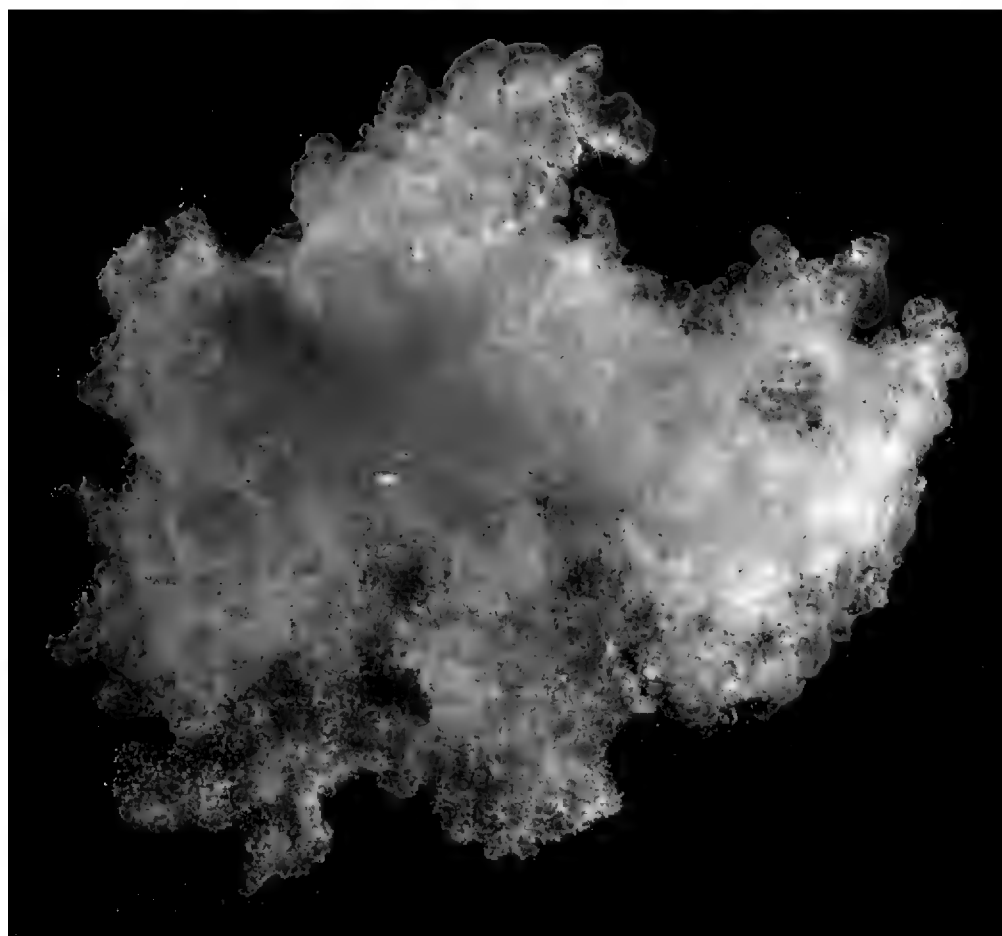


FIGURE 2. *Pseudotetraspora marina*. DLB8366: Algal plain, seaward Media Luna Reef. Field = approximately 5.0 cm.

**Habitat and Comments:** *Pseudotetraspora marina* has rarely been collected in Puerto Rico. The species usually occurs in shallow subtidal saltmarshes, mangroves, and seagrass beds; however, *P. marina* was found in deeper water in Mexico, dredged at 20–29 m depths (Mateo-Cid et al. 2013). The species is extremely common as an epiphyte on seagrass leaves in the Ancote Anchorage (south of Tampa on the western Gulf Coast, SW Gulf of Mexico;

Ballantine and Humm 1975). Woelkerling (1975) concluded *P. marina* and *P. antillarum* were conspecific. However, considering the geographical, climate, and ecological differences of their type localities, the taxonomic status and phylogenetic relationship of the cold temperate Norway *P. marina* (generitype) and the tropical Bahamian *P. antillarum* should be genetically tested. [Additional illustrations: Afonso-Carrillo et al. 2007: figs. 1–3.]

## ULVOPHYCEAE K. R. MATTOX ET K. D. STEWART

### BRYOPSIDOPHYCEAE BESSEY

### BRYOPSIDALES J. H. SCHAFFN.

### BRYOPSIDINEAE HILLIS-COLVINAUX EX VERBRUGGEN ET GUIRY

### BRYOPSIDACEAE BORY

### *Bryopsis* J. V. Lamour.

*Bryopsis* J. V. Lamour. 1809: 333.

Gametophytic thalli are erect, attached below by rhizoids. The thallus consists of a variably cylindrical distinct axis that is oppositely, more or less radially or irregularly branched, with pinnate, radial, or unilateral branchlets, often feather-like in appearance. Axes and branchlets are coenocytic, and chloroplasts possess a single pyrenoid. Asexual reproduction is by fragmentation, aplanospores, and regeneration from extruded protoplasts. Life histories are usually an alternation of filamentous gametophytic macrothalli and sporophytic microthalli of either creeping or erect filaments. Three species and 2 varieties of the 56 currently accepted species of *Bryopsis* occur in Puerto Rico.

## KEY TO THE *BRYOPSIS* SPECIES OF PUERTO RICO

1. Ultimate branchlets surrounding the main axis ..... *B. hypnoides*  
     Ultimate branchlets arranged in 1 or 2 rows ..... 2
2. Frond triangular to lanceolate; branchlets mostly in 2 rows ..... *B. plumosa*  
     Frond linear-lanceolate; branchlets in 1 or 2 rows ..... *B. pennata*

### *Bryopsis hypnoides* J. V. Lamour.

FIGURE 3

*Bryopsis hypnoides* J. V. Lamour. 1809: 333.

**Puerto Rican Records:** Diaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

**Western Atlantic Distribution:** Belize, Costa Rica, Panama, North America, Bermuda, Cuba, Martinique, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, Brazil, Uruguay, Venezuela.  
**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Sète [formerly Cette], Hérault Department, Mediterranean coast of France.

Thalli are somewhat pyramidal in overall shape, to 10 cm or more tall; attached below by prostrate rhizoidal branches. Main axes, 80–140 µm diam, are spirally or irregularly branched in 1 to several orders. Branchlets possess constricted bases and measure 40–80 µm diam. Algae are light green to olive green in color.

**Habitat and Comments:** *Bryopsis hypnoides* is common on mangrove roots, in seagrass beds, and in exposed, shallow-water habitats to 1.0 m depth. [Additional illustrations: Vickers 1908: pl. 53; Littler et al. 2008: 205; Cormaci et al. 2014: 210FP, figs. 1–3.]





FIGURE 3. *Bryopsis hypnoides*. MDP2656: Intertidal, Cabo Rojo lighthouse. Scale bar = 2.0 cm.

***Bryopsis pennata* J. V. Lamour. var. *pennata***

FIGURE 4A

*Bryopsis pennata* J. V. Lamour. 1809: 333, pl. 3: fig. 1a,b.

*Synonym:* *Bryopsis plumosa* var. *pennata* (J. V. Lamour.) Børgesen 1911: 147.

*Puerto Rican Records:* As *Bryopsis pennata*: Taylor 1960; Almodóvar 1962, 1964a, 1964b; Schwartz and Almodóvar 1971; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Costa Rica, Panama, North America, Bermuda, Bahamas, Barbados, Cuba, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, St. Eustatius, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Guyana, Uruguay, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Antilles, West Indies.

*Bryopsis pennata* is the generitype species. Thalli are feather-like and linear-lanceolate in overall shape. Often occurring in large tufts, algae reach 2.0–7.0(–10) cm tall and 5.0–8.0 mm broad. Main axes, 240–360  $\mu\text{m}$  diam, are sparingly branched in upper portions, and lower portions are naked. Algae are attached by rhizoidal holdfasts. Distichous determinate branchlets are contracted at their bases, more or less of uniform length and 75–150  $\mu\text{m}$  diam. Algae are glossy dark green in color, sometimes iridescent.

*Habitat and Comments:* *Bryopsis pennata* usually occurs on hard substrata in quiet-water habitats of the intertidal to shallow subtidal. [Additional illustrations: Harvey 1858: pl. 45A; Norris 2010: fig. 37; Vickers 1908: pl. 52; Cormaci et al. 2014: FP213, figs. 2–3.]

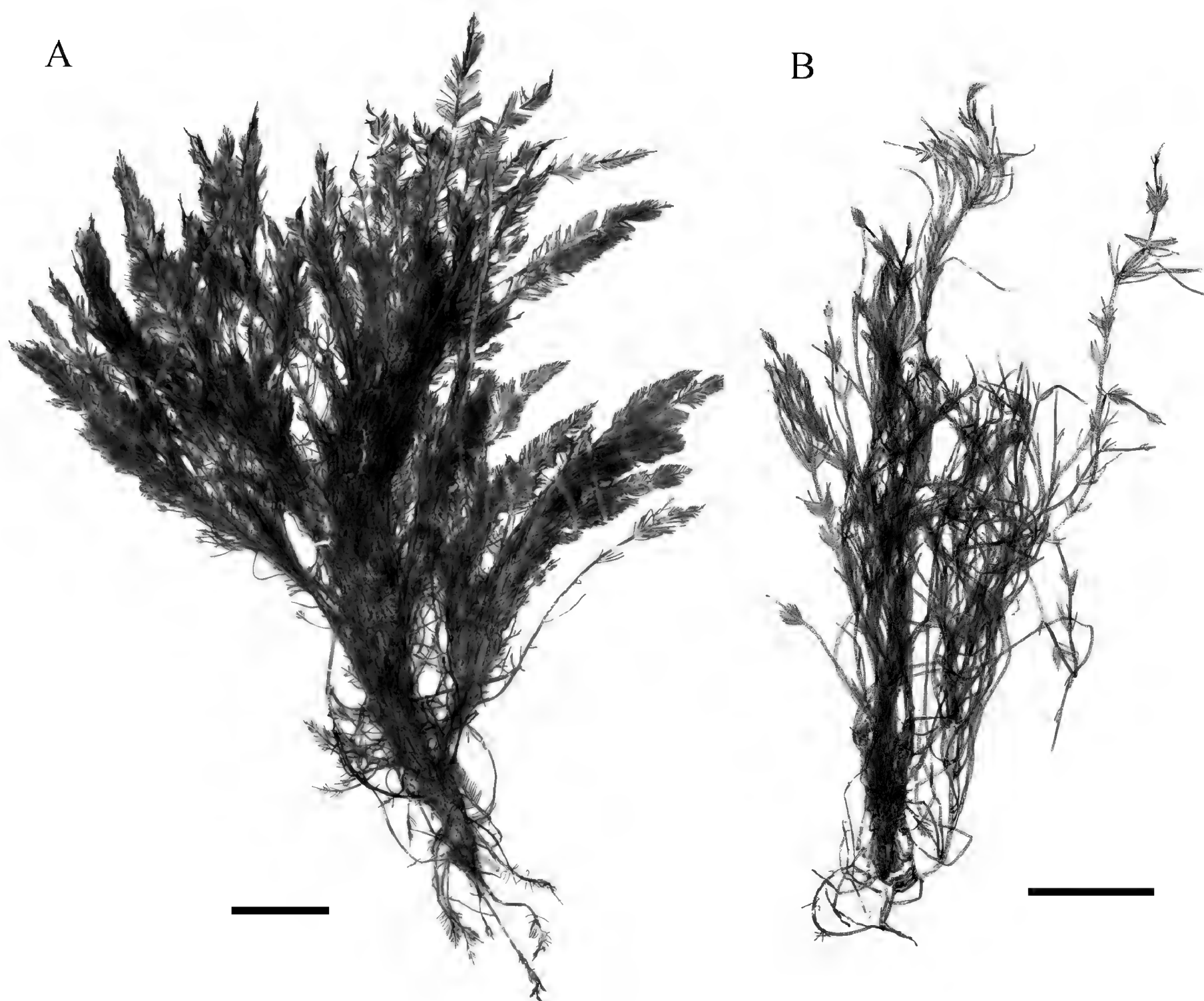


FIGURE 4. *Bryopsis pennata*. (A) *B. pennata* var. *pennata*. DLBsn, herbarium specimen: Cabo Rojo lighthouse, 1.0–2.0 m. Scale bar = 1.0 cm. (B) *B. pennata* var. *lepreurii*. DLB425, herbarium specimen: Cabo Rojo lighthouse, intertidal. Scale bar = 1.0 cm.

***Bryopsis pennata* var. *leprieurii* (Kütz.) Collins et Herv.**

FIGURE 4B

*Bryopsis pennata* var. *leprieurii* (Kütz.) Collins et Herv. 1917: 62.*Basionym*: *Bryopsis leprieurii* Kütz. 1849: 490.*Puerto Rican Records*: The variety is newly recorded for Puerto Rico herein: DLB425, intertidal, Cabo Rojo lighthouse, SW coast of Puerto Rico, (26.X.1979, US Alg. Coll. 218529).*Western Atlantic Distribution*: Bermuda, Guyana, Puerto Rico.*World Distribution*: See Guiry and Guiry (2022).*Type Locality*: Cayenne, French Guiana.

*Bryopsis pennata* var. *leprieurii* differs from *B. pennata* var. *pennata* in having only a few branchlets that occur in discontinuous series. [Additional illustration: as *Bryopsis leprieurii*, Vickers 1908: pl. 50.]

***Bryopsis pennata* var. *secunda* (Harv.) Collins et Herv.***Bryopsis pennata* var. *secunda* (Harv.) Collins et Herv. 1917: 62.*Basionym*: *Bryopsis plumosa* var. *secunda* Harv. 1858: 31, pl. XLV. A: figs. 1–3.*Heterotypic Synonym*: *Bryopsis harveyana* J. Agardh 1887: 22–23.*Puerto Rican Records*: Herein recorded as new to Puerto Rico: DLBsn, intertidal, Cabo Rojo lighthouse, SW coast of Puerto Rico, 26.X.1979, US Alg. Coll. 218530).*Western Atlantic Distribution*: Mexico, North America, Bermuda, Cuba, Martinique, Puerto Rico, Brazil, Venezuela.*World Distribution*: See Guiry and Guiry (2022).*Syntype Localities*: Key West and Sand Key, Florida Keys, Monroe County, Florida.

As the varietal epithet implies, *Bryopsis pennata* var. *secunda* differs from *B. pennata* var. *pennata* by its unilateral or secund nature of the branchlet arrangement. Silva et al. (1996) noted that *B. harveyana* J. Agardh (1887), described from Florida, was a possible synonym of *B. pennata* var. *secunda*. Wynne (2017) and Guiry and Guiry (2022), however, treated the taxon as *B. pennata* var. *secunda*. [Illustrations: as *B. harveyana*, Vickers 1908: pl. 51; Børgesen 1946: fig. 13.]

***Bryopsis plumosa* (Huds.) C. Agardh***Bryopsis plumosa* (Huds.) C. Agardh 1823: 448.*Basionym*: *Ulva plumosa* Huds. 1778: 571.*Puerto Rican Records*: As *Bryopsis plumosa*: Diaz-Piferrer 1963; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine and Aponte 1997a, 2002.*Western Atlantic Distribution*: Belize, Costa Rica, Panama, North America, Bermuda, Bahamas, Barbados, Antigua, Cuba, Grenadines, Martinique, Netherlands Antilles, Puerto

Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Uruguay, Venezuela, Argentina.

*World Distribution*: See Guiry and Guiry (2022).*Type Locality*: Exmouth, Devon, England, UK.

Erect branched axes, reaching up to 5.0–10(–20) cm tall, are distichously branched in 1–3 orders. Fronds are narrowly pyramidal, 1.0–1.5(–3.0) cm broad; arising from prostrate rhizoidal branches. Main axes are naked below, up to 200 µm in diam, tapering distally. Branchlets are sharply constricted at their bases, 65–100 µm diam, and are up to 5.0 mm in length. Algae are light green to olive green in color, sometimes iridescent.

*Habitat and Comments*: *Bryopsis plumosa* grows in protected to partially exposed subtidal habitats. Although generally considered a subtropical to temperate species, the species is widespread in distribution from boreal seas to the tropics (Guiry and Guiry 2022). [Illustrations: Braune and Guiry 2011: fig. 17.2; Cormaci et al. 2014: FP213, fig. 4.]

***Pseudobryopsis* Berthold***Pseudobryopsis* Berthold in Oltmanns 1904

Gametophytic siphonous macrothalli reach up to 20 cm tall above a creeping rhizoidal network. The primary erect axes, simple or rarely dichotomously or subdichotomously branched, taper to the apices and possess dense radial lateral branchlets. Gametangia are borne singly or many on the lower half of the branchlets. Chloroplasts are small, discoid to ellipsoid, usually 1.0–5.0 µm long. Eight species comprise *Pseudobryopsis*, one of which is known from Puerto Rico.

***Pseudobryopsis blomquistii* Díaz-Pif.**

FIGURE 5

*Pseudobryopsis blomquistii* Díaz-Pif. 1965: 464, figs. 1–10.*Synonym*: *Trichosolen blomquistii* (Díaz-Pif.) D. M. John 1977: 407.*Puerto Rican Records*: As *Pseudobryopsis blomquistii*: Diaz-Piferrer 1965; Almodóvar and Ballantine 1983; Ballantine and Aponte 2002. As *Trichosolen blomquistii*: John 1977; Ballantine and Aponte 1997a.*Western Atlantic Distribution*: Mexico, Puerto Rico.*Type Locality*: Punta Arenas, Mayagüez, west coast of Puerto Rico.

Thalli measure up to 8.5–20 cm tall, with numerous erect axes arising from a basal rhizoidal network. Erect axes, 420–870 µm diam, are usually dichotomously branched with dense radially placed unbranched determinate branchlets. Branchlets, 140–340 µm long, are slightly to considerably inflated and septate proximally, 38–53 µm diam at the inflated base and 13–16 µm diam distally with rounded apices. Chloroplasts are discoid, averaging 2.7 µm diam,



with a pyrenoid. Gametangia are ovate to obovate, 30–66  $\mu\text{m}$  diam and 72–125  $\mu\text{m}$  long, and basally septate. They are borne on pedicels laterally in groups of 1–3 on the lower half of each branchlet and develop rounded, terminal papillae with maturity.

*Habitat and Comments:* Although described from Puerto Rico, *Pseudobryopsis blomquistii* is not commonly collected locally. The distinctiveness of *Pseudobryopsis* and *Trichosolen* has been questioned, with Taylor (1962a) and John (1977) concluding the two are congeneric. Nevertheless, Henne and Schnetter (1999) distinguished them on the basis of morphological differences, regarding *Pseudobryopsis* as distinct on the basis of its smaller chloroplasts that lack pyrenoids and gametangia separated from the vegetative supporting branch by a plug.

### ***Trichosolen* Mont.**

*Trichosolen* Mont. 1861: 171.

Coenocytic thalli are from less than 5.0 to more than 20 cm tall, arising from a shared rhizoidal holdfast. Thalli consist of 1 to several simple to infrequently branched main axes that are covered with short branchlets that also may rebranch; these are constricted basally. Algae possess large chloroplasts with pyrenoids. Gametangia are not separated by septa. Two of the 10 known species of *Trichosolen* occur in Puerto Rico. See comments under *Pseudobryopsis blomquistii* concerning the distinctiveness of *Pseudobryopsis* and *Trichosolen*.



FIGURE 5. *Pseudobryopsis blomquistii*. MDP1947, herbarium specimen: Punta Arenas, Mayagüez. Isotype specimen: US Alg. Coll. 083132. Scale bar = 2.0 cm.

KEY TO THE *TRICHOSOLEN* SPECIES OF PUERTO RICO

1. Thalli 10–20 cm tall; 0.75 to 1.25 mm diam . . . . . *T. duchassaingii*  
 Thalli less than 10 cm tall and less than 875  $\mu$ m diam . . . . . *T. longipedicellata*

***Trichosolen duchassaingii* (J. Agardh) W. R. Taylor**

FIGURE 6

*Trichosolen duchassaingii* (J. Agardh) W. R. Taylor 1962a: 62.

*Basionym*: *Bryopsis duchassaingii* J. Agardh 1854: 107.

*Puerto Rican Records*: As *Trichosolen duchassaingii*: Ballantine and Aponte 1997a, 2002. As *Bryopsis duchassaingii*: Diaz-Piferrer 1963.

*Western Atlantic Distribution*: Costa Rica, Mexico, North America, Bermuda, Bahamas, Barbados, Cayman Islands, Cuba, Guadeloupe, Hispaniola, Jamaica, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands.

*Type Locality*: Guadeloupe.

Thalli are soft and lubricous, 10–20 cm tall, with dichotomously divided main axes, 0.75–1.25 mm diam. Erect axes give rise to abundant short slender branchlets, 1.0–2.5 mm long and 20–50(–75)  $\mu$ m diam. Chloroplasts average 9.9  $\mu$ m long and 7.8  $\mu$ m wide. Algae are light yellowish green in color.

*Habitat and Comments*: *Trichosolen duchassaingii* occurs in shallow protected habitats, including lagoons, and margins of mangrove stands. The species has been observed to form extensive blooms following passage of hurricanes in damaged reef habitats in La Parguera. These blooms persisted for approximately one month, covering corals and other substrata in shallow fore reef habitats. These phenomena are also recognized circumtropically for *Trichosolen* species following hurricanes or substantial physical impact to coral reefs in the western Atlantic (Woodley et al. 1981; Littler et al. 1987) and following cyclones in the Pacific (Littler and Littler 1999). Pauly et al. (2011) suggested that nutrients released during catastrophic coral reef events were important to the development of bloom events. Propagules of the alga presumably exist in a cryptic and unrecognized state during nonbloom periods. [Additional illustrations: Littler et al. 2008: 210.]

***Trichosolen longipedicellatus* (H. L. Blomq. et Diaz-Pif.) D. M. John**

*Trichosolen longipedicellatus* (H. L. Blomq. et Diaz-Pif.) D. M. John 1977: 407.

*Basionym*: *Pseudobryopsis longipedicellata* H. L. Blomq. et Diaz-Pif. 1961: 390, figs. 1–8.

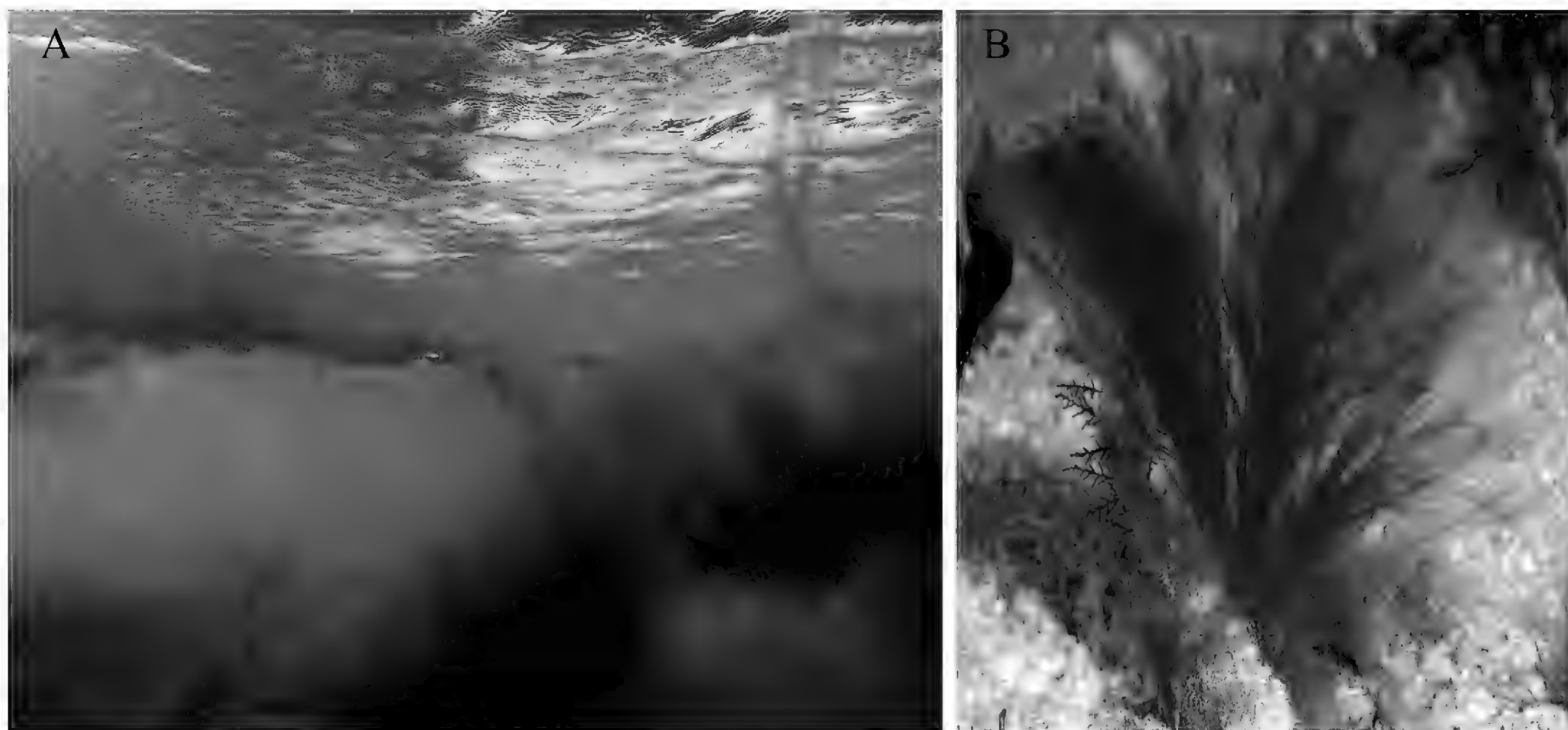


FIGURE 6. *Trichosolen duchassaingii*. (A) Bloom condition, shallow water in lee of Turrumote Reef, La Parguera. Field = approximately 0.75 m. (B) Individual plant, approximately 8.0 cm tall.

*Puerto Rican Records:* As *Trichosolen longipedicellatus*: Ballantine and Aponte 2002. As *Pseudobryopsis longipedicellata*: Blomquist and Diaz-Piferrer 1961; Diaz-Piferrer 1965; Almodóvar and Ballantine 1983.

*Western Atlantic Distribution:* Puerto Rico, Netherlands Antilles.  
*Type Locality:* 1.0 km offshore from Punta Arenas, Mayagüez.

Thalli consist of erect tufts composed of numerous axes, up to 8.5 cm tall. Dichotomously branched axes measure 420–870 µm diam and are densely beset with simple determinate branchlets, 140–340 µm long, that are inflated proximally. Branchlets are septate at their bases, 38–53 µm diam proximally and 13–16 µm diam distally, with rounded apices. Chloroplasts average 11.4 µm long and 8.6 µm wide. Gametangia, measuring 30–66 µm diam and 72–125 µm long, are borne laterally on pedicels, singly or in groups to 3, on the lower half of determinate branchlets.

*Habitat and Comments:* *Trichosolen longipedicellatus* occurs from the intertidal into the subtidal, down to 15 m. The type collection of *Pseudobryopsis longipedicellata* was dredged in 10–15 m depths. This species was also collected at Punta Arenas in shallower water as well as intertidally. Taylor (1962c) and Dawes and Mathieson (2008) regarded this species as a synonym of *T. duchassaingii*; however, others (e.g., Stegenga and Vroman 1988; Henne and Schnetter 1999; Wynne 2005, 2017) recognized the two as distinct species.

## HALIMEDINEAE HILLIS-COL. EX VERBRUGGEN ET GUIRY

### CAULERPACEAE KÜTZ.

#### *Caulerpa* J. V. Lamour.

*Caulerpa* J. V. Lamour. 1809: 332.

Thalli are coenocytic with a creeping stolon or rhizome that gives rise to erect determinate branches (assimilators) and

to descending rhizoids. Assimilators range from being simple filaments to elaborately branched structures. The branchlets are terete, compressed or flattened and simple or divided. Algae possess numerous chloroplasts and amyloplasts, a cell wall composed mainly of xylan, and an elaborate internal network of trabeculae. Growth is apical and indeterminate.

Asexual reproduction occurs by fragmentation. Sexual reproduction, where known, is either holocarpic, where the thallus remains unmodified, no cross walls are formed, and anisogametes are extruded in gelatinous strands through numerous discharge papillae on the siphon wall, or nonholocarpic, where lobed structures are specialized reproduction organs.

*Notes:* High morphological variability among many of the species has made identification of some taxa difficult, and some species have numerous varieties and forms. Børgesen (1907: 379, in reference to *Caulerpa racemosa*) observed that in recognition of varieties, the characters, although useful to recognize forms or varieties, were sometimes very similar or intergrading, and these taxa certainly should not be considered as species. Taylor (1960) similarly noted that many of these morphological characters have unequal systematic value but have descriptive value. Because of this, we have chosen to retain some form and varietal names, even though they have been shown to be conspecific with their nominate species. Huisman (2015) has pointed out that species discrimination (as in this treatment) is based largely on erect branch and branchlet morphologies. Because of the existence of morphological plasticity, in some cases a continuous morphological gradation between species may occur. As a result, molecular analyses are increasingly important in delimiting species. Members of *Caulerpa* occur from the intertidal to depths of at least 100 m (Littler et al. 1986; Norris and Olsen 1991; Ballantine et al. 2016). Puerto Rican *Caulerpa* species are divided into three subgenera (see Draisma et al. 2014). Ninety-seven species of *Caulerpa* are currently recognized worldwide. There are 19 *Caulerpa* species and 12 intraspecific taxa in Puerto Rico.

### KEY TO THE CAULERPA SPECIES OF PUERTO RICO

1. Assimilators lacking branchlets ..... 2  
Assimilators possessing branchlets that are differentiated from assimilators ..... 3
2. Rhizomes and erect portions differentiated, thalli to greater than 15 cm in height ..... *C. wysorii*  
Rhizomes and erect portions similar in form, thalli 3.0 cm tall or less ..... *C. fastigiata*
3. Erect assimilators or branchlets flat or strongly compressed ..... 4  
Erect assimilators not as above ..... 8
4. Erect assimilators bladelike and mostly entire ..... 5  
Erect assimilators not as above ..... 6
5. Assimilator blades 0.5–4.0 cm long and 0.5–4.0 mm wide; blade apices may possess an apical notch, and younger blades may be marginally serrate ..... *C. parvifolia*  
Assimilator blades 3.0–15 cm long and 3.0–13 mm wide ..... *C. prolifera*
6. Erect assimilators compressed with serrate margins, frequently twisted ..... *C. serrulata*  
Erect assimilators pinnately branched with compressed to flattened branchlets ..... 7
7. Bearing broad and flat branchlets, not constricted at their bases ..... *C. mexicana*  
Branchlets compressed, not broad, constricted at their bases ..... *C. taxifolia*

8. Branchlets with smooth, rounded or flattened tips ..... 9  
    Branchlets with aculeate tips ..... 13
9. Branchlets cylindrical ..... 10  
    Branchlets spherical, clavate, or peltate, not cylindrical ..... 12
10. Thalli larger, with 7.0–18 mm long cylindrical branchlets ..... *C. ashmeadii*  
    Thalli smaller, 1.0–2.0 cm tall; branchlets either spherical or regularly or occasionally forked ..... 11
11. Nearly sessile; spherical branchlets, 0.9–2.4 mm diameter, crowded on short assimilators, less than 10 mm high .....  
    ..... *C. microphysa*  
    Branchlets cylindrical in 2 rows, rarely radial ..... *C. vickersiae*
12. Branchlets nearly spherical or sharply swollen or swollen or spherical on elongate bases or abruptly truncated and peltate .  
    ..... *C. chemnitzia/C. racemosa*<sup>1</sup>  
    Branchlets abruptly truncated, peltate with slight scalloping on the margins; proliferating branchlets frequently originate  
    from the center of the peltate branchlets ..... *C. nummularia*
13. Branchlets arranged in verticils (whorls) ..... 14  
    Branchlets not arranged in verticils (whorls) ..... 15
14. Stolons tomentose; assimilators sharply constricted at their forks; singular tuft or growing in patches (not spreading) ..  
    ..... *C. webbiana*  
    Stolons not tomentose; assimilators without constrictions; may form a spreading carpet on the substratum .....  
    ..... *C. verticillata*
15. Stolons tomentose ..... *C. pusilla*  
    Stolons not tomentose ..... 16
16. Branchlets slightly curved and closely placed around the assimilators ..... *C. lanuginosa*  
    Branchlets not as above ..... 17
17. Branchlets toothlike, in 2 to 5 ranks ..... *C. cupressoides*  
    Branchlets cylindrical, 3.0–11 mm long, in 2 ranks ..... *C. sertularioides*

<sup>1</sup> Many of the varieties formerly assigned to *Caulerpa racemosa* have been shown molecularly to be aligned with *C. chemnitzia*.

### ***Caulerpa* subgen. *Caulerpa***

*Caulerpa* subgen. *Caulerpa*.

Thalli possess glabrous or pubescent stolons. In some species, the stolons are covered densely by rhizoids. Assimilator branchlets are distinctly different from the rhizoids or other stolon appendages. Chloroplasts possess pyrenoids in some of the species, whereas other species lack associated pyrenoids.

### ***Caulerpa ashmeadii* Harv.**

FIGURE 7

*Caulerpa ashmeadii* Harv. 1858: 18, pl. 38A.

*Puerto Rican Records:* Ballantine 1977; Almodóvar et al. 1979; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Mexico, North America, Bermuda, Cuba, Martinique, Nevis, Puerto Rico, U.S. Virgin Islands, Brazil, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Key West, Florida Keys, Monroe County, Florida, USA.

Thalli are large with assimilators originating from elongate rhizomes, to 2.0 m long and 2.0–2.5 mm diam. The rhizomes are attached in loose sediment by abundant rhizoids. Assimilators measure 10–30 cm tall and 1.5–2.0 mm diam. They are branched distichously in 2 rows of cylindrical branchlets, 0.5–1.5 mm diam and 10–18 mm long, and possess blunt, clavate or rounded tips.

*Habitat and Comments:* *Caulerpa ashmeadii* occurs on sandy or muddy bottoms or in seagrass beds, from 3 to 40 m depths. The species is common at the Media Luna and Margarita algal plains in 17 and 24 m depths, respectively. In the Florida Keys it also occurs in deep water, 40–60 depths (Leichter et al. 2008). This taxon is one of the *Caulerpa* species found to produce natural products that act as chemical defenses (Paul et al. 1987). [Additional illustrations: Taylor 1960: pl. 11: fig. 4, pl. 18: fig. 9; Littler and Littler 2000: 359.]

### ***Caulerpa chemnitzia* (Esper) J. V. Lamour. var. *chemnitzia***

*Caulerpa chemnitzia* (Esper) J. V. Lamour. 1809: 332.

*Basionym:* *Fucus chemnitzia* Esper 1800: 167 [erroneously printed as p. 127], pl. 88: figs. 1, 4–6.

*Puerto Rican Records:* Puerto Rican reports of the species are as varieties; see below.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Malabar Coast, Arabian Sea, SW coast of India, northern Indian Ocean.



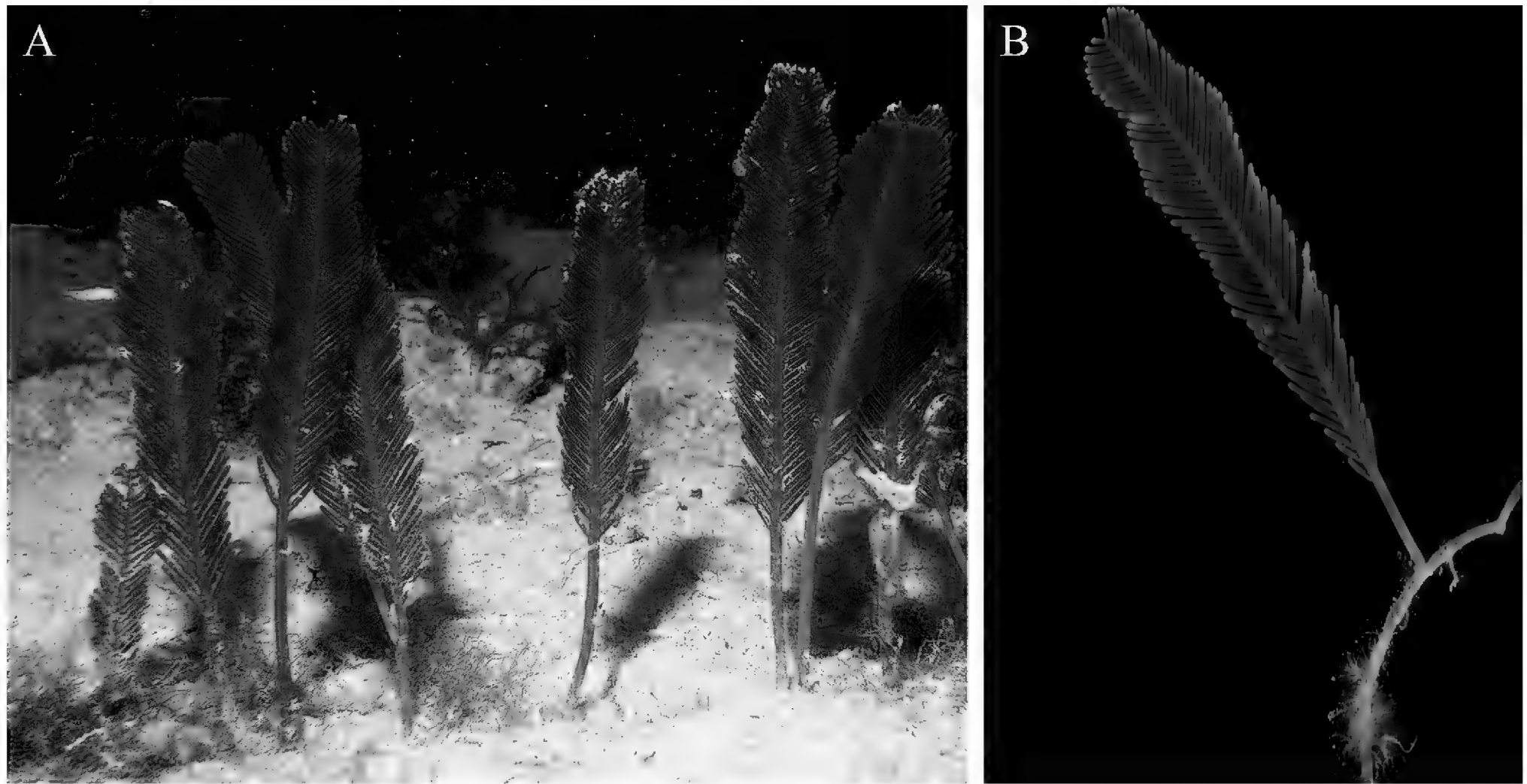


FIGURE 7. *Caulerpa ashmeadii*. (A) In situ habit photograph from algal plain, seaward Media Luna Reef, La Parguera, 17 m. Field = approximately 8.0 cm. (B) Close-up of erect assimilator with opposite cylindrical branchlets. Field = approximately 6.0 cm.

In Puerto Rico three distinct morphological forms of *C. chemnitzia* occur (all previously considered to be varieties of *C. racemosa*). In their circumscription of *Caulerpa chemnitzia* based on genetic analyses that included taxa that showed a continuous morphological gradient between them, Belton et al. (2014) concluded that the species is broadly defined and did not recognize varieties. Norris et al. (2017) in their treatment of *Caulerpa chemnitzia* in the Gulf of California chose to acknowledge the different morphologies in the genus as varieties. We follow that approach in recognizing the potential ecological significance of these differences. Specimens corresponding to *Caulerpa chemnitzia* var. *chemnitzia* have not been recognized for Puerto Rico. See Belton et al. (2014: fig. 8E) for an illustration of the holotype.

***Caulerpa chemnitzia* var. *laetevirens* (Mont.)  
Fern. García et Riosmena**

FIGURE 8B

*Caulerpa chemnitzia* var. *laetevirens* (Mont.) Fernández-García et Riosmena in Norris et al. 2017: 87.

*Basionym*: *Caulerpa laetevirens* Mont. 1842a: 13.

*Puerto Rican Records*: Herein recorded as new to Puerto Rico: MDP2043, Pitahaya (W of La Parguera), shallow water (20. VI.1963, MSM 16232).

*Western Atlantic Distribution*: Florida, Bahamas, Puerto Rico.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Toud Island (Warrior Islet), Torres Strait, Australia.

Thalli are robust, with assimilators 12–30 cm tall. Branchlets are either densely imbricate or widely spaced. Assimilators of the Puerto Rican plant are the latter, possessing branchlets that are elongate and subcylindrical with rounded apices. [Additional illustrations: Littler et al. 2008: 218.]

***Caulerpa chemnitzia* var. *occidentalis* J. Agardh**

FIGURE 8A

*Caulerpa chemnitzia* var. *occidentalis* J. Agardh 1873: 37 (as *C. chemnitzia* f. *occidentalis*).

*Synonym*: *Caulerpa racemosa* var. *occidentalis* (J. Agardh) Borgesen 1907: 379, figs. 28, 29 (see Belton et al. 2014: 48).

*Puerto Rican Record*: As *Caulerpa racemosa* var. *occidentalis*: Almodóvar 1962.

*Western Atlantic Distribution*: Panama, North America, Bermuda, Bahamas, Cuba, Martinique, Puerto Rico, U.S. Virgin Islands, Brazil, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Syntype Localities:* “ß, ad oras calidiores atlanticas Americae a sinu superiore Mexicano saltem ad Pernambucco usque descendens” (Agardh 1873: 37); upper Gulf of Mexico to Pernambuco, Brazil [Veracruz, Mexico, Gulf of Mexico, fide Belton et al. (2014: fig. S4B)].

*Lectotype Locality:* Vera Cruz, Mexico, Gulf of Mexico (Belton et al. 2014). Specimen LD-16789, cited by Belton et al. (2014), could be a possible lectotype (see Habitat and Comments section below).

Cylindrical assimilators reach up to 15 cm tall and 1.3–1.6 mm diam. The branchlets are radially situated along the axes and borne on assimilators, 2.0–3.0 mm in length and expanding distally to 1.5–2.5 mm diam to subspherical to spherical apices, 2.0–4.0 mm diam. Rhizomes are 2.0–3.0 mm diam.

*Habitat and Comments:* In Puerto Rico, *Caulerpa chemnitzia* var. *occidentalis* generally occurs in calm, shallow waters on rocks, coral reefs, mangrove prop roots, and offshore algal plains. Belton et al. (2014: 48, fig. 8C) concluded *C. chemnitzia*

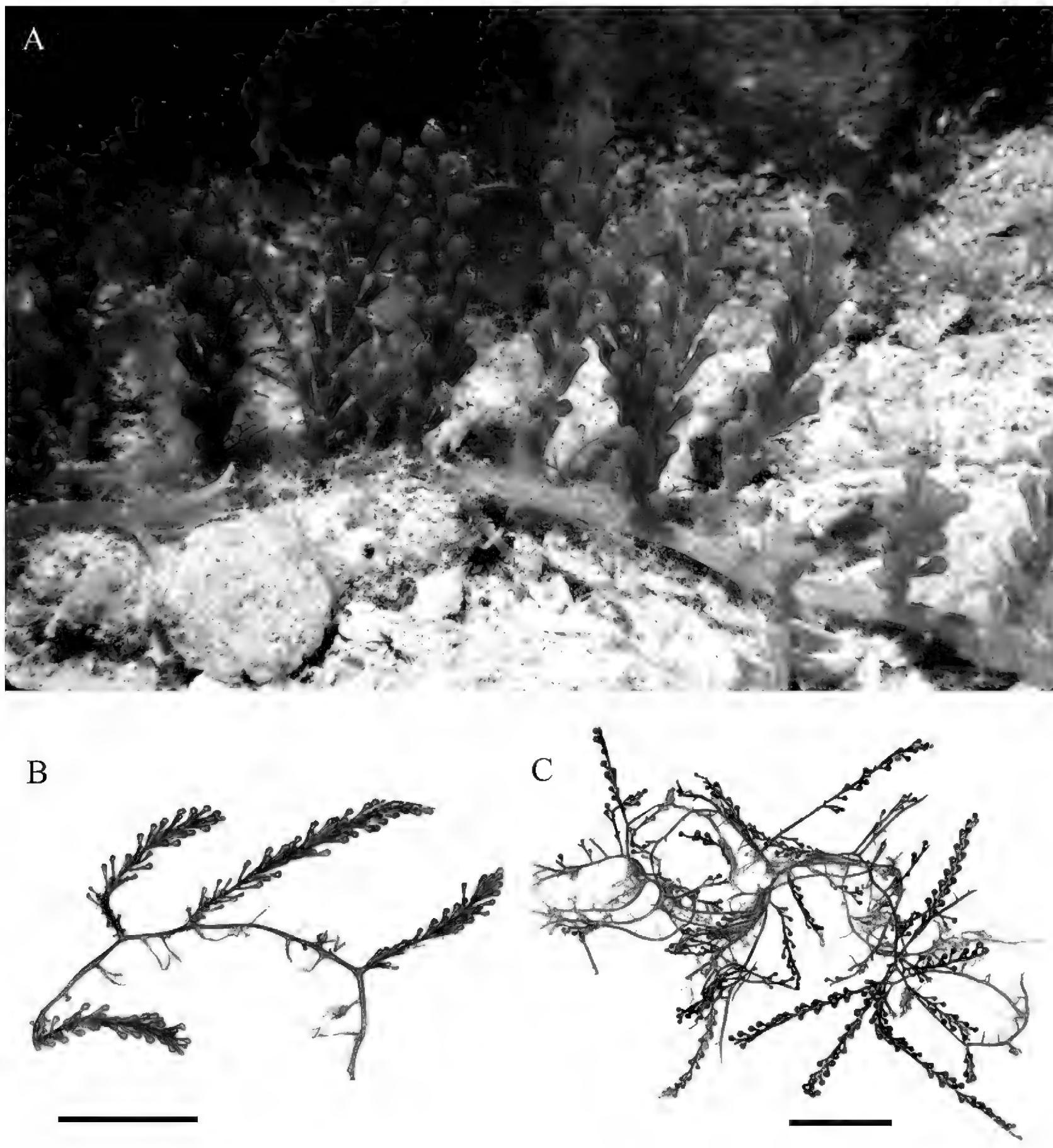


FIGURE 8. *Caulerpa chemnitzia*. (A) *C. chemnitzia* var. *occidentalis*. In situ habit photograph from algal plain, seaward Media Luna Reef, La Parguera, 17 m. Field = approximately 8.0 cm. (B). *C. chemnitzia* var. *laetevirens*. MDP2043, herbarium specimen: Pitahaya, La Parguera, 0.5 m. Scale bar = 2.0 cm. (C) *C. chemnitzia* var. *peltata*. DLBsn, herbarium specimen: Magueyes Island, La Parguera. Scale bar = 2.0 cm.

var. *occidentalis* J. Agardh (1873) and *C. racemosa* var. *occidentalis* (J. Agardh) Børgesen (1907) were heterotypic synonyms of *C. chemnitzia*. A syntype specimen of *C. racemosa* var. *occidentalis* (LD-16789) documented by Belton et al. (2014: figs. 54, 54B) is considered to be a lectotype. Originally described as *C. chemnitzia* var. *occidentalis* J. Agardh from a folder in Herbarium Agardh (LD) labeled “syntypes of  $\beta$  *occidentalis*” and collected from Veracruz (No. 16789), it is now regarded as *C. chemnitzia* (Esper) J. V. Lamouroux (Belton et al. 2014). [Additional illustrations: Børgesen 1913: figs. 123, 124; Taylor 1960: pl. 17: fig. 6; Littler and Littler 2000: 371; Belton et al. 2014: fig. 8C.]

***Caulerpa chemnitzia* var. *peltata*  
(J. V. Lamour.) Zanardini**

FIGURE 8C

*Caulerpa chemnitzia* var. *peltata* (J. V. Lamour.) Zanardini 1858: 287.

*Basionym*: *Caulerpa peltata* J. V. Lamour. 1809: 332.

*Homotypic Synonym*: *Caulerpa racemosa* var. *peltata* (J. V. Lamour.) Eubank in Stephenson 1944: 349, comb. inval.; *Caulerpa racemosa* var. *peltata* (J. V. Lamour.) Eubank 1946: 421, figs. 2r,s.

*Puerto Rican Records*: As *Caulerpa chemnitzia*: Ballantine et al. 2016. As *Caulerpa peltata*: Diaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a.

*Western Atlantic Distribution*: Belize, Costa Rica, Mexico, North America, Bermuda, Bahamas, Barbuda, Cuba, Puerto Rico, Trinidad and Tobago, Brazil, Colombia.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Antilles, West Indies.

Thalli are generally small, arising from divided rhizomes, 1.0–2.0 mm diam, with rhizoids. Erect assimilators reach 5.0–50 mm tall, with 1 or more peltate branchlets borne on slender pedicels, 1.0–2.0 mm in length. Ultimate branchlets are mostly disclike, 1.0–2.0 mm thick and 1.5–8.0 mm wide.

*Habitat and Comments*: *Caulerpa chemnitzia* var. *peltata* occurs on rocks and coral fragments in algal plains in shallow water to 70 m depths (Ballantine et al. 2016, as *C. chemnitzia*). The variety also occurs in the Gulf of Mexico to 73 m depths (Eiseman and Blair 1982) and to 61–73 m depths in the Bahamas (Norris and Olsen 1991).

Caribbean *Caulerpa peltata* and *Caulerpa chemnitzia* J. V. Lamour. have had a long and sometimes confused taxonomic history (Lamouroux 1809; Zanardini 1858; Weber-van Bosse 1898; Børgesen 1925; Gilbert 1942; Eubank 1946; Silva et al. 1996; Verlaque et al. 2003; Dawes and Matheson 2008; Norris 2010; Price 2011; Belton et al. 2014). Belton et al. (2014) concluded *C. peltata*, including *C. racemosa* var. *peltata* (J. V. Lamour.) Eubank, was a heterotypic synonym of *C. chemnitzia* (Esper) J. V. Lamour. (1809). [Additional illustrations: as *Caulerpa chemnitzia* f. *ad peltatam*, Svedelius 1906: figs. 28, 29; as *Caulerpa peltata*, Svedelius 1906: fig. 31; Taylor 1960: pl. 17:

fig. 2, pl. 18: fig. 1; Belton et al. 2014: fig. 2B (Lamouroux’s 1809 illustration); Huisman 2015: pl. 4E.]

***Caulerpa cupressoides* (West ex M. Vahl)  
C. Agardh var. *cupressoides***

FIGURE 9A

*Caulerpa cupressoides* (West ex M. Vahl) C. Agardh 1817: xxii.

*Basionym*: *Fucus cupressoides* M. Vahl 1802: 38.

*Puerto Rican Records*: As *Caulerpa cupressoides*: Almodóvar and Blomquist 1959; Almodóvar 1962, 1964a, 1964b; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution*: Belize, Costa Rica, Mexico, Panama, North America, Bermuda, Bahamas, Barbados, Antigua, Cayman Islands, Cuba, Dominica, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Nevis, Puerto Rico, St. Eustatius, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: St. Croix, U.S. Virgin Islands.

Thalli possess elongate rhizomes, 20–30 cm long and 1.5–2.5 mm diam. Assimilators reach to 25 cm tall and are naked or nearly naked for their proximal 5.0–15 mm. They are rarely simple, more commonly dichotomously branched, bearing short apiculate branchlets in 2 or, most often, 3 ranks. The apiculate branchlets are 1.0–2.0 mm long.

*Habitat and Comments*: In Puerto Rico, *Caulerpa cupressoides* occurs in sandy and muddy bottoms from 1 to 40 m depths and in shallow seagrass beds. [Additional illustrations: Harvey 1858: pl. 39B; Littler et al. 2008: 216.]

***Caulerpa cupressoides* var. *flabellata* Børgesen**

FIGURE 9B,C

*Caulerpa cupressoides* var. *flabellata* Børgesen 1907: 368, figs. 18, 19.

*Puerto Rican Records*: Herein recorded as new to Puerto Rico: DLBsn, seaward Media Luna Reef, 17 m (28.IV.1976, US Alg. Coll. 219635); DLB425, intertidal, Cabo Rojo light-house, SW coast of Puerto Rico (26.X.1979, US Alg. Coll. 218529); DLBsn, seaward Margarita Reef, 24 m (7.X.1983, US Alg. Coll. 219619); DLB1548, 1.6 km seaward Pita Haya, 11 m (12.II.1984, US Alg. Coll. 219617); DLB3964, Islote (Arecibo), 12 m (12.VI.1991, US Alg. Coll. 219631).

*Western Atlantic Distribution*: Belize, Panama, North America, Cuba, Puerto Rico, St. Eustatius, Brazil.

*World Distribution*: See Guiry and Guiry (2022).

*Syntype Localities*: St. John and St. Thomas, U.S. Virgin Islands.



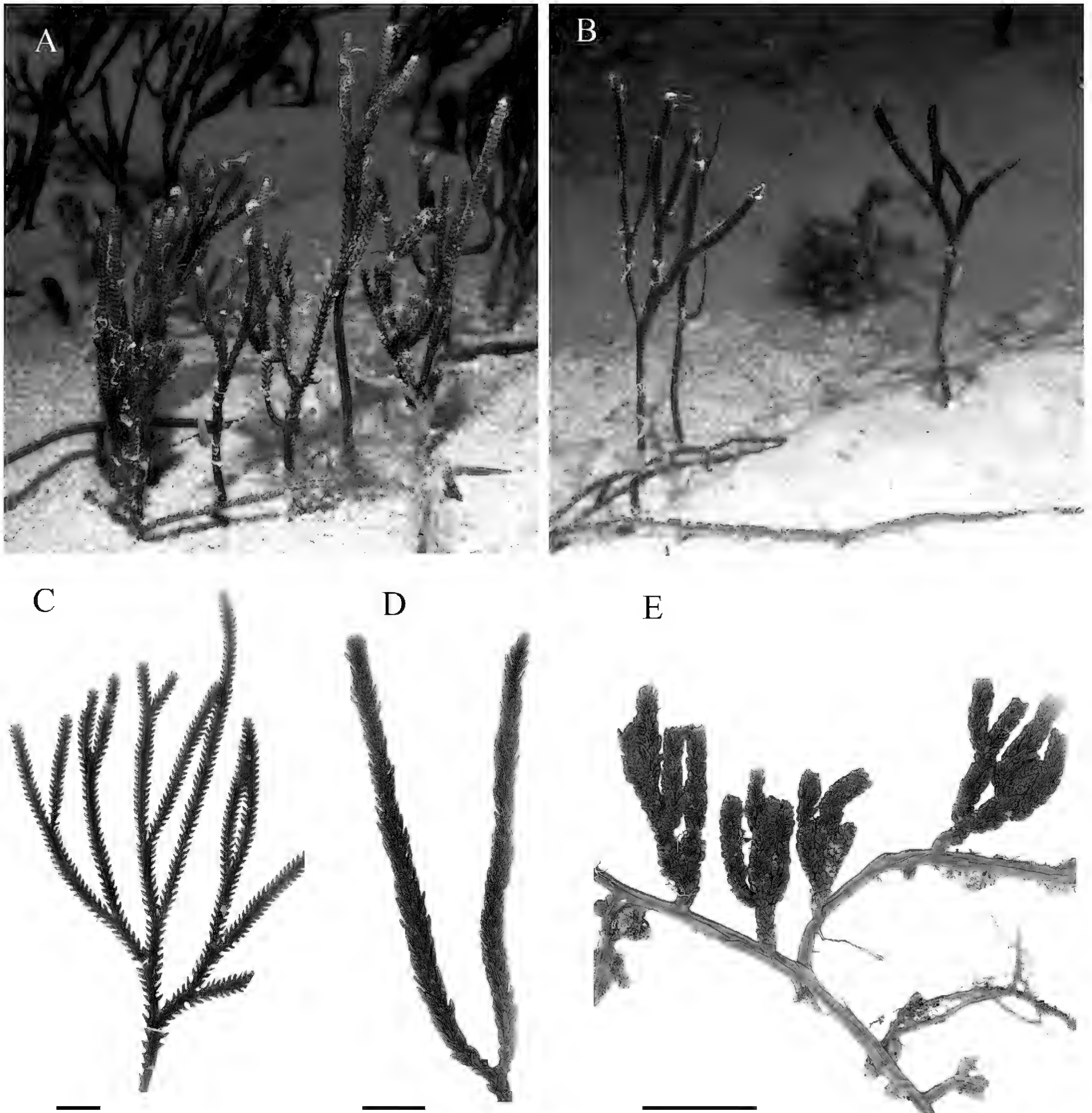


FIGURE 9. *Caulerpa cupressoides*. (A) *C. cupressoides* var. *cupressoides*. In situ habit photograph from algal plain, seaward Media Luna Reef, La Parguera, 17 m. Field = approximately 8.0 cm. (B) *C. cupressoides* var. *flabellata*. Habit same as in A. Field = approximately 8.0 cm. (C) *C. cupressoides* var. *flabellata*. DLB1548, herbarium specimen: Seaward Pita Haya, 11 m. Scale bar = 1.0 cm. (D) *C. cupressoides* var. *lycopodium*. DLB3963, herbarium specimen: Islote, 11 m. Scale bar = 1.0 cm. (E) *C. cupressoides* var. *mamillosa*. DLB1440, herbarium specimen: Esperanza Beach, Manatí, intertidal. Scale bar = 1.0 cm.

Assimilators are erect, compressed to flattened, up to 20 cm tall, and branched dichotomously to irregularly 3–5 times. Assimilators, 1.0–2.0 mm wide, are naked for 3.0–8.0 cm, bear opposite branchlets along their margins in 2 opposite rows. The branchlets are short, often spinelike, up to 1.5 mm long and to 1.0 mm diam, and possess acute apices. Rhizomes measure 2.0–2.5 mm diam.

*Habitat and Comments:* *Caulerpa cupressoides* var. *flabellata*, with its characteristic bilateral branching, occurs in Puerto Rican specimens only from deeper water or shaded habitats, for example, the Margarita algal plain at 24 m depth. Calvert (1976) demonstrated that bilateral symmetry versus radial symmetry is characteristic of *Caulerpa* species growing in deeper water where the light irradiance is reduced. [Additional illustrations: Taylor 1960: pl. 14: figs. 4, 5.]

***Caulerpa cupressoides* var. *lycopodium* Weber Bosse**

FIGURE 9D

*Caulerpa cupressoides* var. *lycopodium* Weber Bosse 1898: 335, pl. XXVII [27], figs. 8–13, pl. XXVIII [28], figs. 10–12, 14.

*Homotypic Synonym:* *Caulerpa lycopodium* C. Agardh 1817: 23, *nom illeg.*

*Puerto Rican Records:* Herein recorded as new to Puerto Rico: DLB22, Islote, intertidal, (1978, US Alg. Coll. 219638); DLB3963, Islote, 11 m, (12.VI.1991, US Alg. Coll. 219632).

*Western Atlantic Distribution:* Bermuda, Barbados, Cuba, Martinique, Puerto Rico, Brazil.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* “E mari Brasiliae et Indiae Occidentalis.”

Rarely branched assimilators are up to 20 cm tall. Branchlets are in 3 ranks and are upturned and cylindrical, 2–6 times as long as the assimilator diameter.

***Caulerpa cupressoides* var. *mamillosa* (Mont.)  
Weber Bosse**

FIGURE 9E

*Caulerpa cupressoides* var. *mamillosa* (Mont.) Weber Bosse 1898: 332, pl. 28: figs. 5–7.

*Basionym:* *Caulerpa mamillosa* Mont. 1842a: 13.

*Puerto Rican Records:* Herein recorded as new to Puerto Rico: DLB1440, Manati, Esperanza Beach, intertidal (20.XII.1983, US Alg. Coll. 219618).

*Western Atlantic Distribution:* North America, Bermuda, Barbados, Cuba, Martinique, Puerto Rico, Brazil.

*World Distribution:* See Guiry and Guiry (2022).

*Syntype Localities:* Agalega Islands; Mangareva, Îles Gambier, French Polynesia (Silva et al. 1996).

Assimilators reach 7.0 cm tall with branchlets occurring in several ranks. The branchlets are obovoid in shape, apically mucronate, and are less than the assimilator diameter in length. [Additional illustrations: Taylor 1960, pl. 15: fig. 4, pl. 18: fig. 11.]

***Caulerpa fastigiata* Mont.**

FIGURE 10

*Caulerpa fastigiata* Mont. 1837: 353.

*Puerto Rican Records:* Diaz-Piferrer 1963; Almodóvar 1964a; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.



FIGURE 10. *Caulerpa fastigiata*. DLBsn, herbarium specimen: White Horse Reef, La Parguera. Scale bar = 1.0 cm.

*Western Atlantic Distribution:* Belize, Panama, North America, Bermuda, Bahamas, Cuba, Hispaniola, Martinique, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Cuba.

Thalli are filamentous with little differentiation between the assimilators and rhizomes. Algae grow in tufts or clumps or form mat-like colonies 1.5–3.0 cm tall. Assimilators, 40–120 µm diam, are branched dichotomously, oppositely or irregularly. Rhizomes measure 150–210 µm diam and possess hairlike rhizoids, 20–60 µm diam.

*Habitat and Comments:* *Caulerpa fastigiata* is most commonly encountered in shallow-water habitats, usually to about 1.0 m depth on muddy and sandy bottoms or on mangrove roots. In southwest Puerto Rico, *C. fastigiata* is common on mangrove (*Rhizophora*) prop roots. [Additional illustrations: Vickers 1908: pl. 36; Børgesen 1911: fig. 1; Taylor 1960: pl. 10: fig. 12; Littler et al. 2008: 217.]

### ***Caulerpa lanuginosa* J. Agardh**

FIGURE 11

*Caulerpa lanuginosa* J. Agardh 1873: 28 [replacement name for *C. lycopodium* Harv. 1858: 19, pl. 37B, *nom. illeg.* (see Silva et al. 1996: 823)].

*Puerto Rican Records:* Almodóvar 1964b; Almodóvar and Blomquist 1965; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* North America, Bahamas, Barbados, Cayman Islands, Cuba, Jamaica, Martinique, Puerto Rico, Brazil, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Key West, Florida Keys, Monroe County, Florida.

Assimilators, 3.0–13 cm tall, are simple or branched and tomentose at the base. Filiform branchlets are randomly distributed about assimilators, measuring 3.0–5.0 mm long and 60–180 µm diam; they are mucronate at the tips. Rhizomes measure to 30 cm in extent and are densely tomentose.

*Habitat and Comments:* The species is typically collected in shallow water on sandy substratum; however, it is also known to 110 m in depth in Puerto Rico (Ballantine et al. 2016). [Additional illustrations: Taylor 1960: pl. 14: figs. 1, 2; Braune and Guiry 2011: fig. 18.8.]

### ***Caulerpa mexicana* Sond. ex Kütz.**

FIGURE 12

*Caulerpa mexicana* Sond. ex Kütz. 1849: 496.

*Heterotypic Synonym:* *Caulerpa crassifolia* (C. Agardh) J. Agardh 1873: 13.

*Puerto Rican Records:* As *Caulerpa mexicana*: Taylor 1960; Almodóvar and Pagán 1971; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016. As *Caulerpa crassifolia*: Howe 1915; Almodóvar and Blomquist 1959, 1961.

*Western Atlantic Distribution:* Belize, Costa Rica, Panama, North America, Bermuda, Bahamas, Antigua, Barbados, Cayman Islands, Cuba, Grenadines, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, St. Eustatius, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Guyana, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Atlantic Coast of Mexico (Lipkin and Silva 2002).

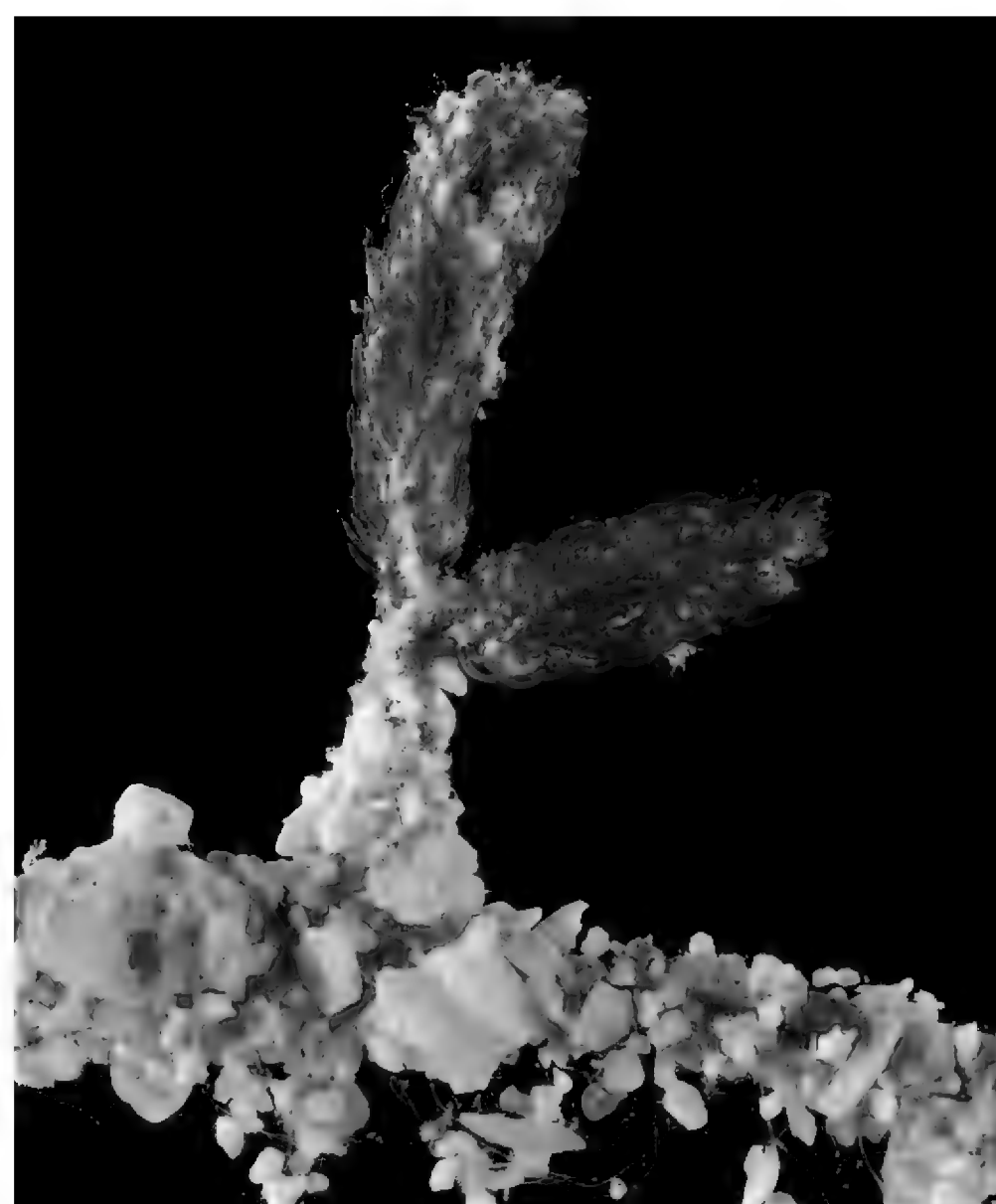


FIGURE 11. *Caulerpa lanuginosa*. Field = approximately 2.5 cm.



Thalli erect, 2.0–25 cm tall. Assimilators possess central flattened axes, 1.0–3.0 mm wide, that bear flattened, oppositely placed, upturned branchlets, 2.0–4.0 mm wide and 2.0–10 mm long, with tapered and acute apices that are not constricted at their base. Assimilators arise from slender rhizomes, 0.5–1.25 mm in diam, that are up to 30 cm in length.

**Habitat and Comments:** In Puerto Rico *Caulerpa mexicana* most commonly occurs on sandy to muddy bottoms in shallow waters of back reefs, seagrass beds, and mangrove habitats. It also is encountered in deeper waters from 36 to 49 m depths (Ballantine et al. 2016). The analyses of Belton et al. (2014) found *C. mexicana* to be one of the species of *Caulerpa* represented by more than one genetic species. Further work is required to resolve their taxonomic status. [Additional illustrations: Harvey 1859: pl. 37A; Littler and Littler 2000: 365.]

### ***Caulerpa microphysa* (Weber Bosse) Feldmann**

FIGURE 13

*Caulerpa microphysa* (Weber Bosse) Feldmann 1955: 430.

**Basionym:** *Caulerpa racemosa* f. *microphysa* Weber Bosse 1898: 361, pl. 33: fig. 5.

**Puerto Rican Records:** As *Caulerpa microphysa*: Taylor 1960; Almodóvar 1962, 1964a, 1964b; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

**Western Atlantic Distribution:** Costa Rica, Panama, North America, Bermuda, Bahamas, Barbados, Bequia, Jamaica, Cuba, Netherlands Antilles, Nevis, Puerto Rico, St. Lucia, Trinidad and Tobago, Brazil, Venezuela.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Makassar (Ujung Pandang), South Sulawesi Province, Sulawesi (island formerly known as Celebes), Indonesia.

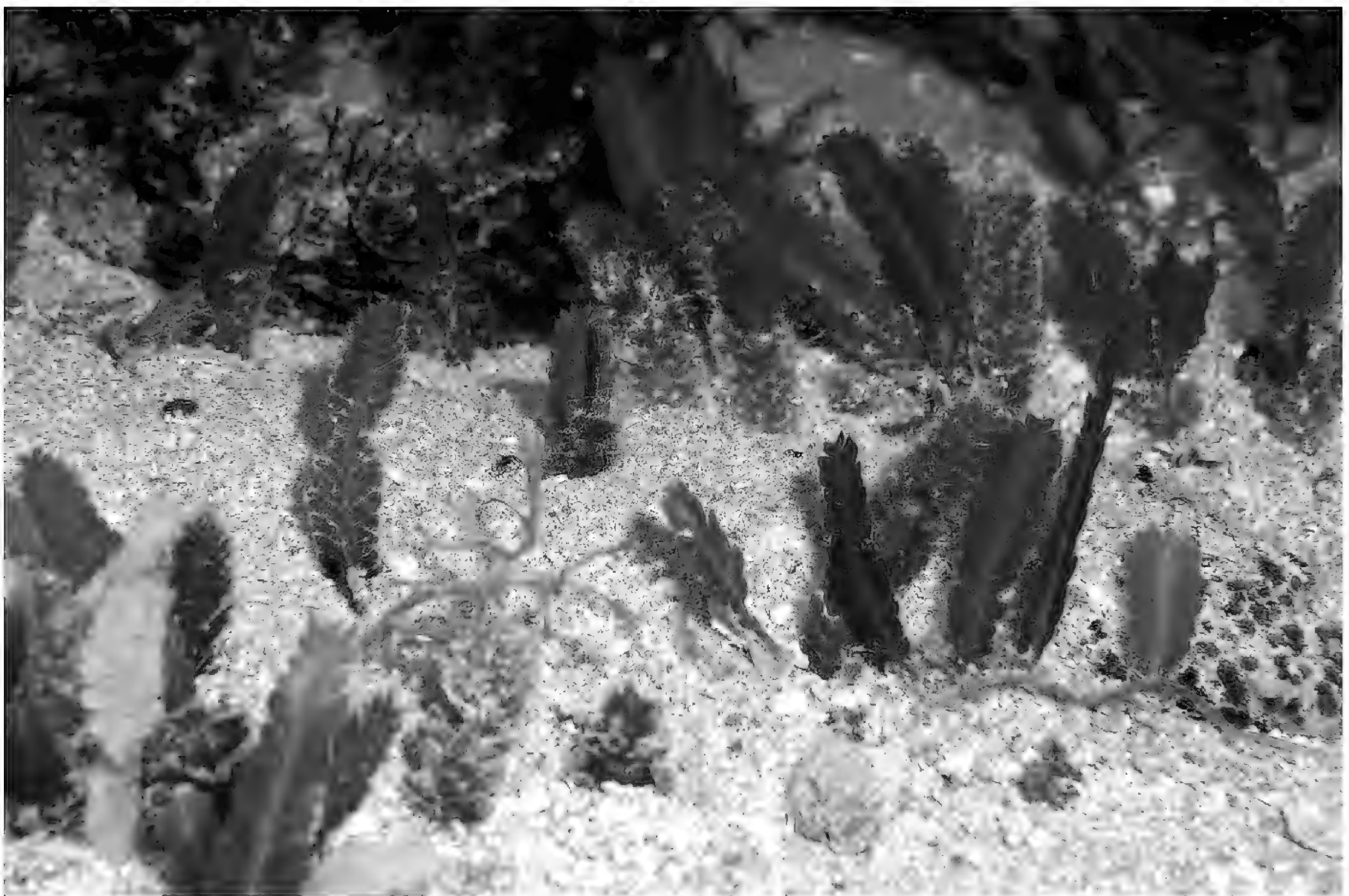


FIGURE 12. *Caulerpa mexicana*. In situ habit photograph from algal plain, seaward Media Luna Reef, La Parguera, 17 m. Field = approximately 10 cm.



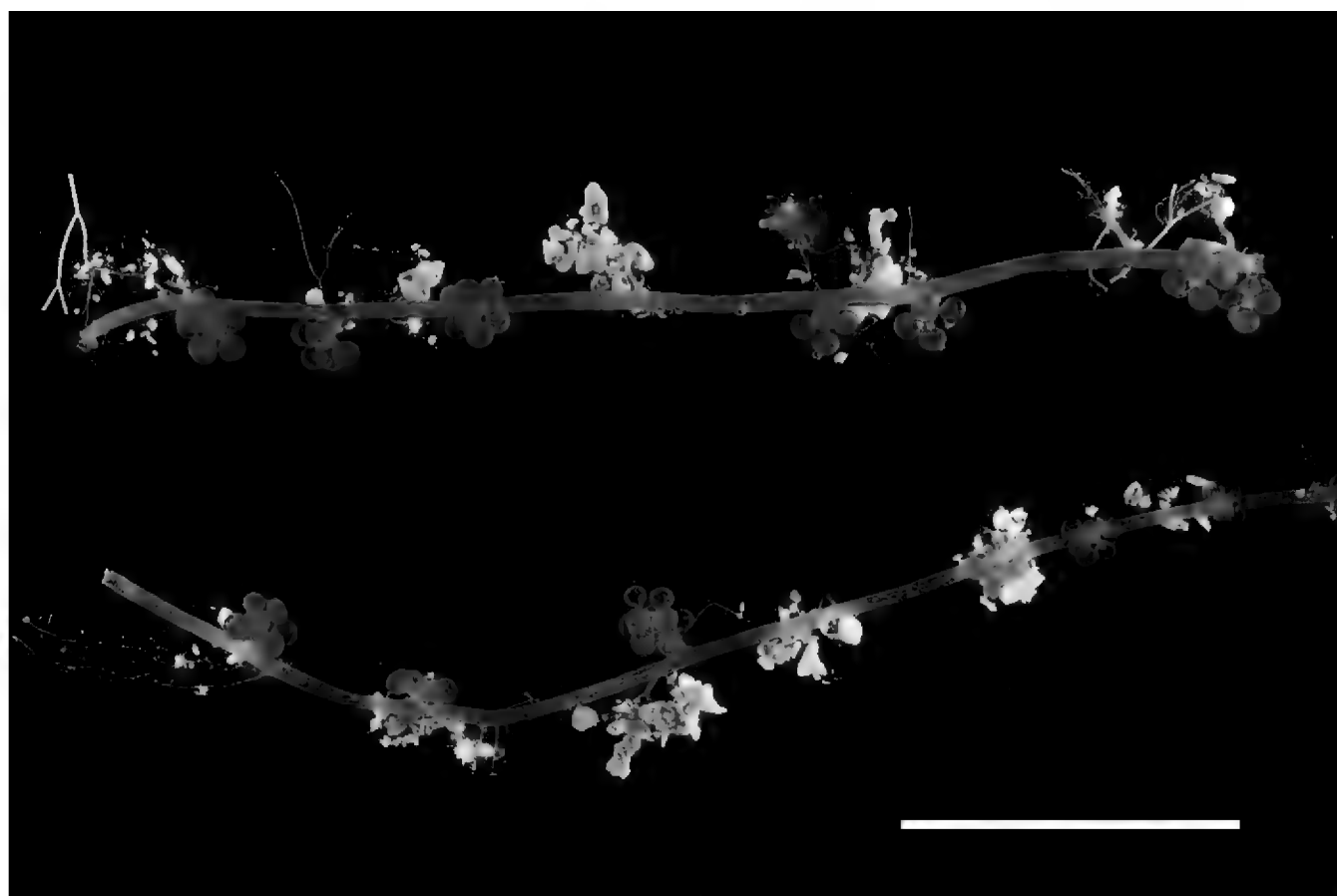


FIGURE 13. *Caulerpa microphysa*. Located 1.5 km seaward Media Luna Reef, 17 m. Scale bar = 10 cm.

Thalli possess assimilators, 3.0–30 mm tall, that bear solitary or clustered (often crowded) spherical branchlets, 0.9–2.4 mm in diameter. These small branchlets are nearly sessile or on stalks up to 0.5 mm long that are often constricted at their distal end just below the spherical branchlet. Assimilators arise from slender, creeping rhizomes with branching rhizoid-like filaments that attach to shell, coral fragments, and sand.

**Habitat and Comments:** *Caulerpa microphysa* is primarily a species found in moderate to deep water, reportedly dredged to 110 m depths (Taylor 1960; Frederick 1963). In Puerto Rico *C. microphysa* commonly grows in coarse sand substratum in deepwater offshore algal plains at 17 and 24 m depths and also occurs in deeper waters from 50 to 82 m (Ballantine et al. 2016). [Additional illustrations: Taylor 1960: pl. 17: fig. 5, pl. 18: fig. 6; Littler et al. 2008: 220.]

### ***Caulerpa nummularia* Harv. ex J. Agardh**

FIGURE 14

*Caulerpa nummularia* Harv. ex J. Agardh 1873: 38.

**Homotypic Synonym:** *Caulerpa peltata* var. *nummularia* (Harv. ex J. Agardh) Weber Bosse 1898.

**Puerto Rican Record:** Ballantine et al. 2004.

**Western Atlantic Distribution:** Belize, Cuba, Puerto Rico.

**World Distribution:** See Guiry and Guiry (2022).

**Syntype Localities:** Friendly Islands (now Tonga) and Nuka Hiva, Marquesas Islands, French Polynesia.

**Lectotype Locality:** Tonga (formerly “Friendly Islands”; Belton et al. 2014: 49, fig. 9, lectotype).

Thalli possess simple or branched assimilators, 5.0–15 cm tall, that bear an initial disclike, peltate branchlet or a linear series of 2 or more disclike branchlets, with each additional disc arising from the center (or edges) of the subtending disc. The stalked peltate branchlets mostly possess scalloped, serrate or incised margins, occasionally smooth and measure up to 4.5 mm diam. Slender rhizomes are up to 0.6 mm diam.

**Habitat and Comments:** *Caulerpa nummularia* bears resemblance to *C. chemnitzia* var. *peltata*; however, it may be differentiated in that the branchlet margins are normally scalloped as opposed to being always smooth in the latter. Furthermore, in *C. nummularia*, branchlets may give rise to additional peltate discs from their center or margin, but that is not so in *C. chemnitzia* var. *peltata*. Caribbean specimens referred to *C. nummularia* will require further molecular systematic study as Belton et al. (2014) noted that the species appears to be restricted to the central Indo-Pacific region. [Additional illustrations: as *Caulerpa peltata* f. ad *nummulariam*, Svedelius 1906: fig. 32; as *Caulerpa nummularia*, Svedelius 1906: figs. 35, 36; Littler and Littler 2000: 365; Huisman et al. 2007: 181; Kraft 2007: fig. 64D,E.]

### ***Caulerpa parvifolia* Harv.**

FIGURE 15

*Caulerpa parvifolia* Harv. 1860: pl. 172.

**Synonym:** *Caulerpa brachypus* f. *parvifolia* (Harvey) A. B. Cribb 1958: 209.

**Puerto Rican Records:** Newly reported herein from Puerto Rico: M&DL30360, as *C. brachypus* var. *parvifolia* (Harvey) A. B. Cribb, NW of Culebra Island, 26 m (3.VI.1995, US Alg. Coll. 227951).

*Western Atlantic Distribution:* North America, Martinique, Puerto Rico.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Kiama, New South Wales, Australia (Silva et al. 1996).

Assimilators are bladelike and unbranched or rarely forked, possessing smooth margins or having small marginal teeth. The blades are sessile or briefly stalked, 0.5–4.0(–8.0) mm long and to 4.0 mm broad. The rhizomes are extensive and measure 80–100(–500). Algae are grass green in color.

*Habitat and Comments:* Cribb (1958) treated *Caulerpa parvifolia* as a forma, *C. brachypus* Harv. f. *parvifolia* (Harv.) Cribb on the basis of its smaller size but otherwise close morphological similarity to the latter species. Littler and Littler (2000) reported the species (also as *Caulerpa brachypus* Harv.) from seagrass beds and deepwater algal plains, to 30 m depth. Jacoby et al. (2004) indicated that *B. brachypus* is not native to the west Atlantic and represents an invasive species on eastern Florida reefs. Belton et al. (2015) demonstrated that there was a molecular distinction between Australian specimens corresponding to two separate taxa, one with the morphology of *C. brachypus* and the other the “*parvifolia*” morphology, and therefore reinstated *C.*

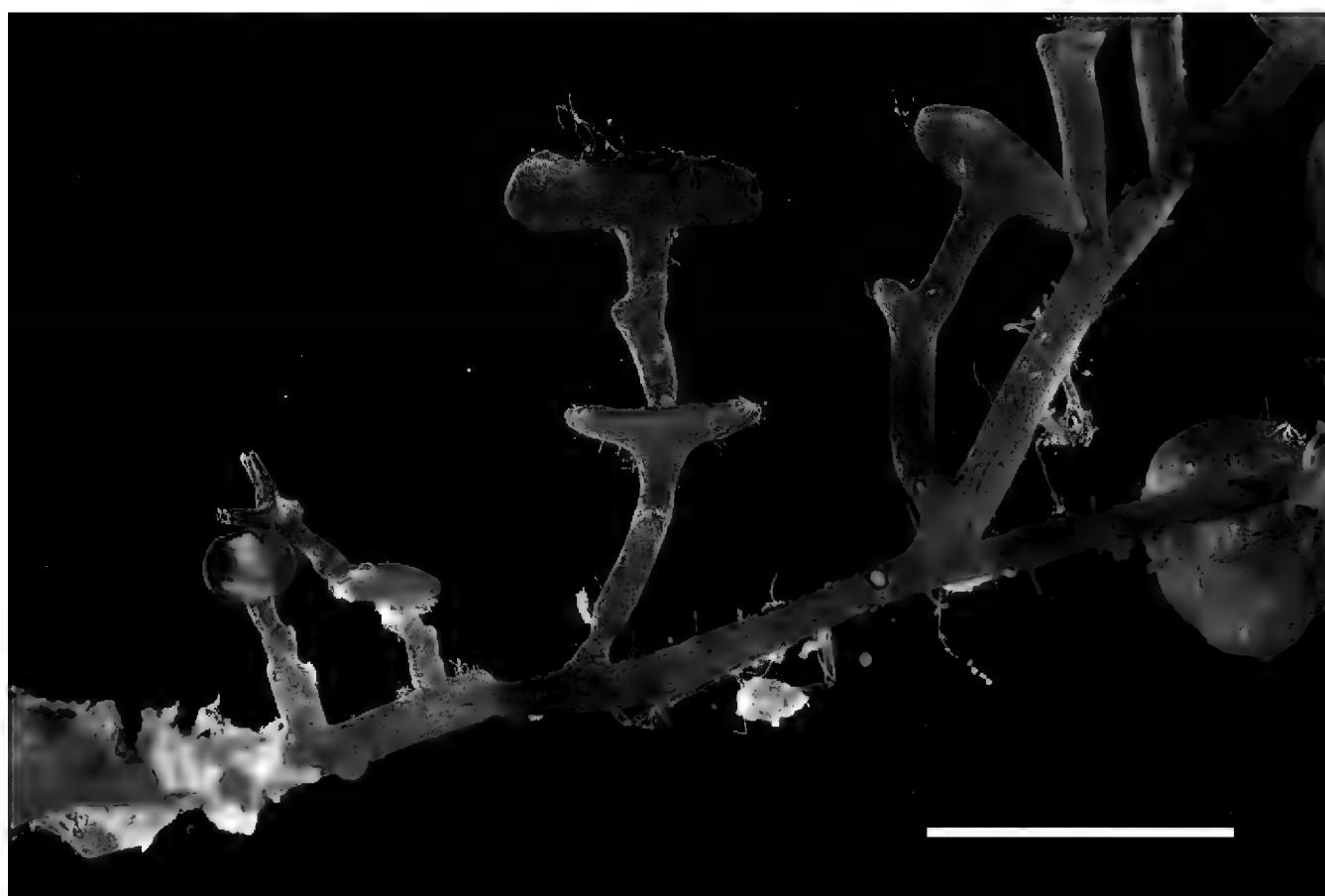


FIGURE 14. *Caulerpa nummularia*. DLB6003: Romero Reef, La Parguera, 8.2 m. Field = approximately 3.0 cm. Scale bar = 5.0 mm.



FIGURE 15. *Caulerpa parvifolia*. D&ML30360, herbarium specimen: Culebra Island, 26 m. Scale bar = 1.0 cm.

*parvifolia*. *Caulerpa parvifolia* is apparently very rare in Puerto Rico, known only from a single collection. [Additional illustrations: as *Caulerpa brachypus* f. *brachypus*: Littler and Littler 2000: 359; Littler et al. 2008: 21.]

***Caulerpa prolifera* (Forssk.) J. V. Lamour. f. *prolifera***

FIGURE 16A

*Caulerpa prolifera* (Forssk.) J. V. Lamour. 1809: 332.

*Basionym*: *Fucus prolifera* Forssk. 1775: 193.

*Puerto Rican Records*: As *Caulerpa prolifera*: Howe 1915; Almodóvar and Blomquist 1961; Almodóvar 1964b; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution*: Costa Rica, Panama, Mexico, North America, Bermuda, Bahamas, Barbados, Cuba, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, St. Eustatius, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Alexandria, Egypt, Mediterranean Sea; lectotype selected by Egerod (1952).

*Caulerpa prolifera* is the generitype species. Large colonies often form from extensive subsediment rhizomes, 1.0–1.5 mm

diam. Assimilators are terete below, 0.5–1.0 cm long and 1.0–1.4 mm diam, and develop into single flat blades. The blades are linear to lanceolate, sometimes proliferous, measuring 3.0–15 cm tall and 7.0–20 mm wide. Apices are narrow to obtuse; blades not uncommonly bear similar proliferations from their face or margin.

*Habitat and Comments*: *Caulerpa prolifera* is often common and can form large colonies in sandy or muddy bottoms of shallow-water seagrass beds and lagoons. In the Florida Keys, the species occurs in deep water, 40–70 depths (Leichter et al. 2008). [Additional illustrations: Harvey 1858: pl. 38B; Littler and Littler 2008: 221.]

***Caulerpa prolifera* f. *zosterifolia* Børgesen**

FIGURE 16B

*Caulerpa prolifera* f. *zosterifolia* Børgesen 1907: 359, fig. 6.

*Puerto Rican Records*: Almodóvar and Blomquist 1961; Almodóvar 1964b.

*Western Atlantic Distribution*: Panama, North America, Bermuda, Puerto Rico, U.S. Virgin Islands.

*World Distribution*: See Guiry and Guiry (2022) and Gonzalez Henriquez and Santos Guerra (1983).

*Type Locality*: Lagoon of Krause, St. Croix, U.S. Virgin Islands (Boisset and Ferrer-Gallego 2015).

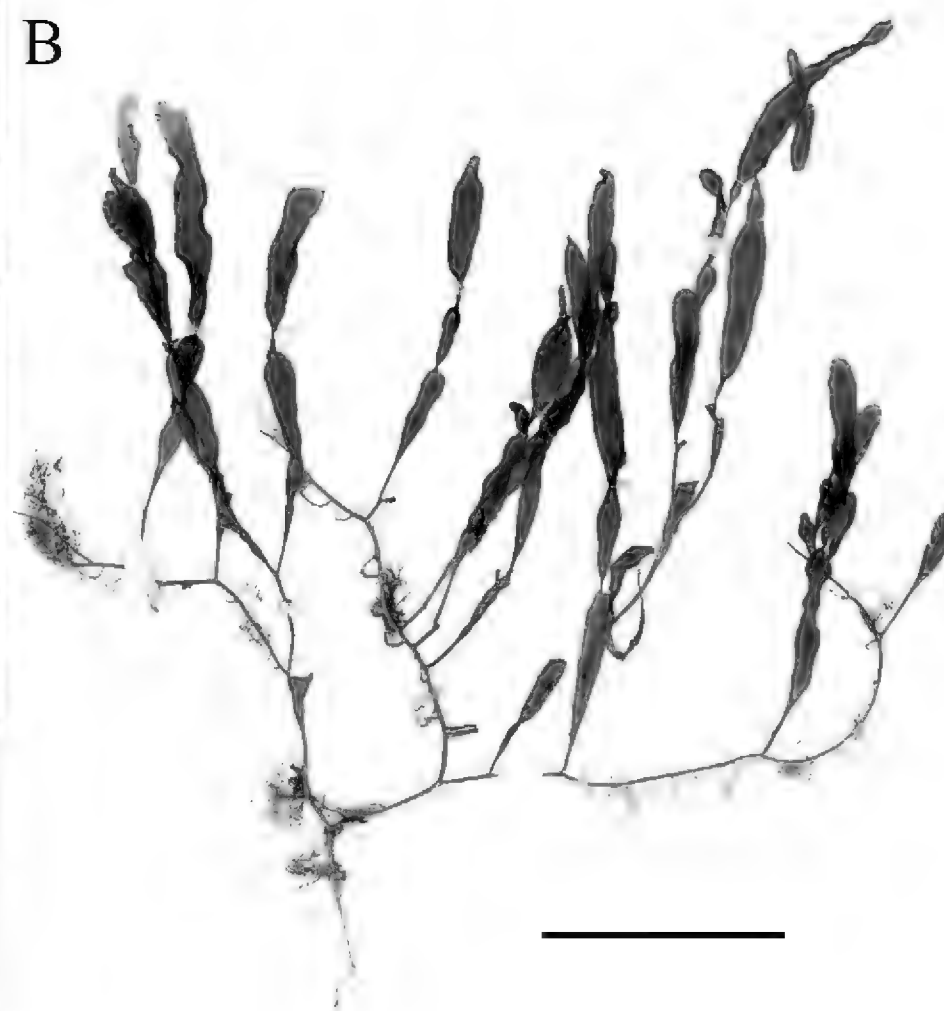
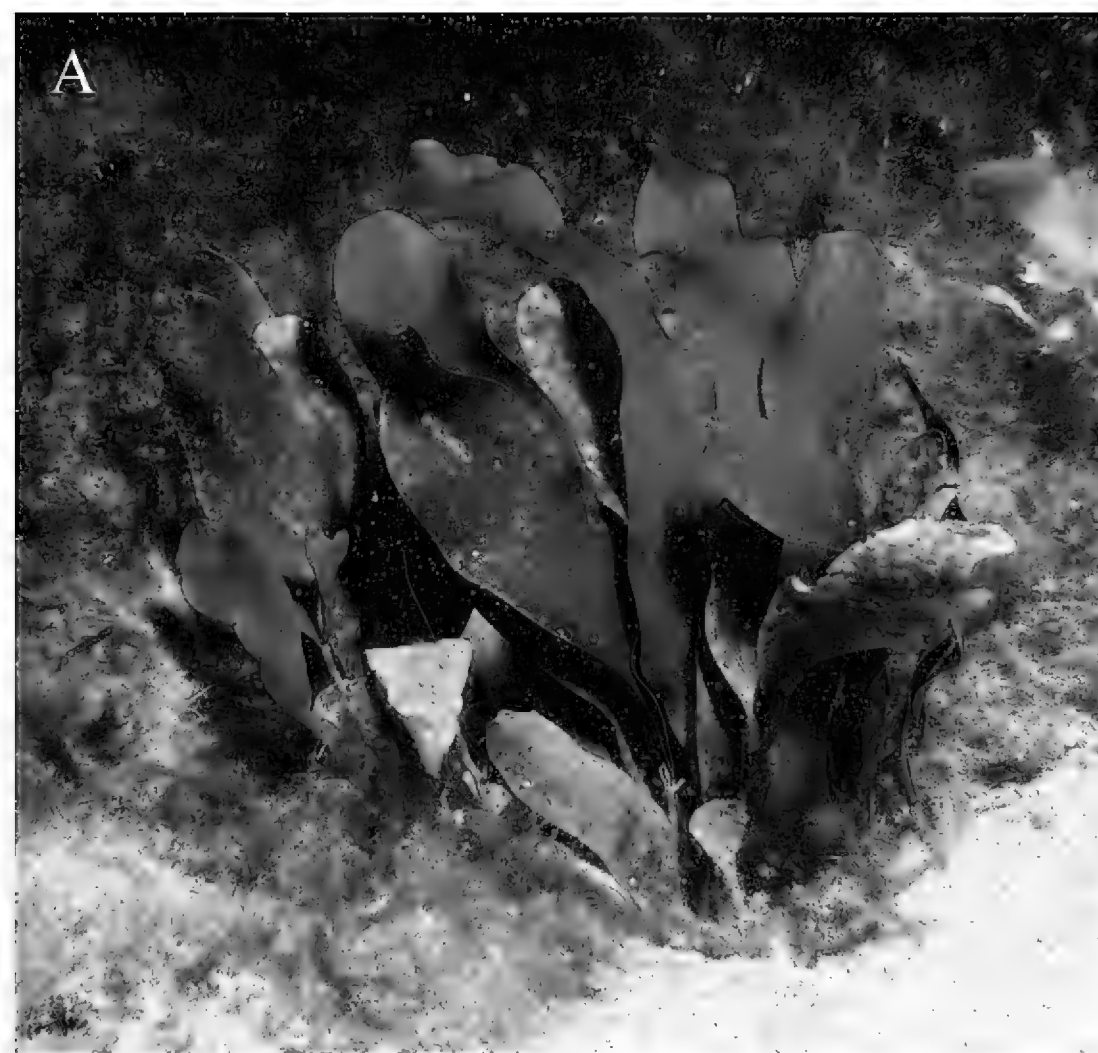


FIGURE 16. *Caulerpa prolifera*. (A) *C. prolifera* var. *prolifera*. In situ habit photograph from seagrass bed off Pitahaya, La Parguera, 17 m. Field = approximately 7.0 cm. (B) *C. prolifera* f. *zosterifolia*. DLB5778, herbarium specimen: Guayacan Island, 1.0 m. Scale bar = 5.0 cm.

*Caulerpa prolifera* f. *zosterifolia* is typically a more delicate form, with narrower linear-lanceolate blades, 6.0 mm or less wide, and more highly proliferously branched than *C. prolifera* f. *prolifera*.

**Habitat and Comments:** *Caulerpa prolifera* f. *zosterifolia* typically occurs in reduced-light, shallow-water habitats. [Additional illustration: Børgesen 1913: 127, fig. 101.]

***Caulerpa racemosa* (Forssk.) J. Agardh var. *racemosa***

FIGURE 17A

*Caulerpa racemosa* (Forssk.) J. Agardh 1873: 35.

**Basionym:** *Fucus ramosus* Forssk. 1775: 191.

**Puerto Rican Records:** As *Caulerpa racemosa*: Howe 1915; Almodóvar and Blomquist 1959; Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar 1962, 1964a, 1964b, 1971; Almodóvar and Pagán 1971; Almodóvar and Rehm 1971; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002; Ruiz and Ballantine 2009; Ballantine et al. 2016.

**Western Atlantic Distribution:** Belize, Panama, Costa Rica, Mexico, North America, Bermuda, Bahamas, Antigua, Bequia, Cayman Islands, Cuba, Dominica, Grenadines, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, St. Kitts, St. Lucia, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Suez, north coast of Gulf of Suez, northeast Egypt, Red Sea.

Thalli form colonies to 2.0 m in extent with long, coarse branching rhizomes, 2.0–3.0 mm diam. The assimilators are 1.0–5.0 cm tall and produce clusters of spherical, ovate, or clavate stalked branchlets that are 2.0–4.0 mm diam and borne on 1.0–2.0 mm long stalks. The branchlets are typically radially branched but can be variably arranged. Spherical branchlets of live specimens sometimes possess a centrally placed whitish dot. Algae are grass green in color.

**Habitat and Comments:** In Puerto Rico, *Caulerpa racemosa* is a common species in the intertidal and shallow waters of exposed reef flats, seagrass meadows, and mangrove habitats. Although less common in deeper waters, it also occurs on offshore algal plains as well as down to 50 m depths (Ballantine et al. 2016). Leichter et al. (2008) also report the species to 40–60 m depths in the Florida Keys. Almodóvar and Rehm (1971) reported *C. racemosa* to form ball-shaped growths in the lee of Collado Reef, La Parguera. [Additional illustration: Belton et al. 2014: fig. 1A (upper right).]

***Caulerpa racemosa* var. *macrophysa* (Sond. ex Kütz.) W. R. Taylor**

FIGURE 17B

*Caulerpa racemosa* var. *macrophysa* (Sond. ex Kütz.) W. R. Taylor 1928: 101, pl. 12: fig. 3.

**Basionym:** *Chauvinia macrophysa* Sond. ex Kütz. 1857: 6, pl. 15: fig. 2.

**Synonyms:** *Caulerpa macrophysa* (Sond. ex Kütz.) G. Murray 1887: 38; *Caulerpa racemosa* var. *clavifera* f. *macrophysa* (Sond. ex Kütz.) Weber-van Bosse 1898: 361, pl. 33: fig. 4; *Caulerpa racemosa* f. *macrophysa* (Sond. ex Kütz.) Sved. 1906: 120, fig. 13, nom. illeg.

**Puerto Rican Records:** Herein recorded as new to Puerto Rico: LRA4506, Cayo Fanduca, Puerto Real (14.V.1962, US Alg. Coll. 218529); LRA4711, Aguirre (12.XI.1962, US Alg. Coll. 51950); LRA7126, Punta Verraco, Guayanilla (11.VIII.1974, US Alg. Coll. 55774); DLB54555, Papayo, La Parguera, (14.XI.2000, US Alg. Coll. 219778).

**Western Atlantic Distribution:** Panama, North America, Cuba, Martinique, Netherlands Antilles, Puerto Rico, Brazil, Venezuela.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Central America, eastern Pacific (Verlaque et al. 2003). Note that Indonesia is given by Abbott and Huisman (2004).

Assimilators are erect and up to 6.0 cm tall with axes that bear scattered to tight clusters of subspherical to spherical branchlets, 3.0–7.0 mm diam, and often have a mottled or spotted appearance. The branchlets are borne on short stalks, (1.0–)2.0 mm in length, although sometimes stalks may be absent or not apparent. Branching rhizomes are 3.0–4.0 mm diam, with rhizoids at the base measuring 2.0 mm diam, becoming narrower. The growing tips are often yellowish.

**Habitat and Comments:** In Puerto Rico, *Caulerpa racemosa* var. *macrophysa* occurs on rock or limestone in shallow reefs, usually in habitats with moderate wave energy. Taxonomic debate continues as to whether *C. macrophysa* should be recognized as an independent species (e.g., Abbott and Huisman 2004; Hodgson et al. 2004; Dawes and Mathieson 2008), a variety (e.g., Taylor 1960; Wynne 2011a), or a synonym of *C. racemosa* (Belton et al. 2014). Littler and Littler (2000: 357) recognized *C. macrophysa* and noted its branchlet morphology and mottled or spotted pigmentation distinguished it from *C. racemosa*. Belton et al. (2014) were unable to locate the type specimen of *Chauvinia macrophysa* Sonder ex Kütz. (1857) to resolve its relationship to *C. racemosa* but stated these two taxa were likely conspecific. As with *Caulerpa chemnitzia*, we recognize the descriptive value of stable morphological expressions, and in this treatment, we list the variety. [Additional illustrations: Taylor 1960: pl. 17: fig. 1, pl. 18: fig. 2; Littler and Littler 2000: 363; Belton et al. 2014: 50, fig. 10B,D.]



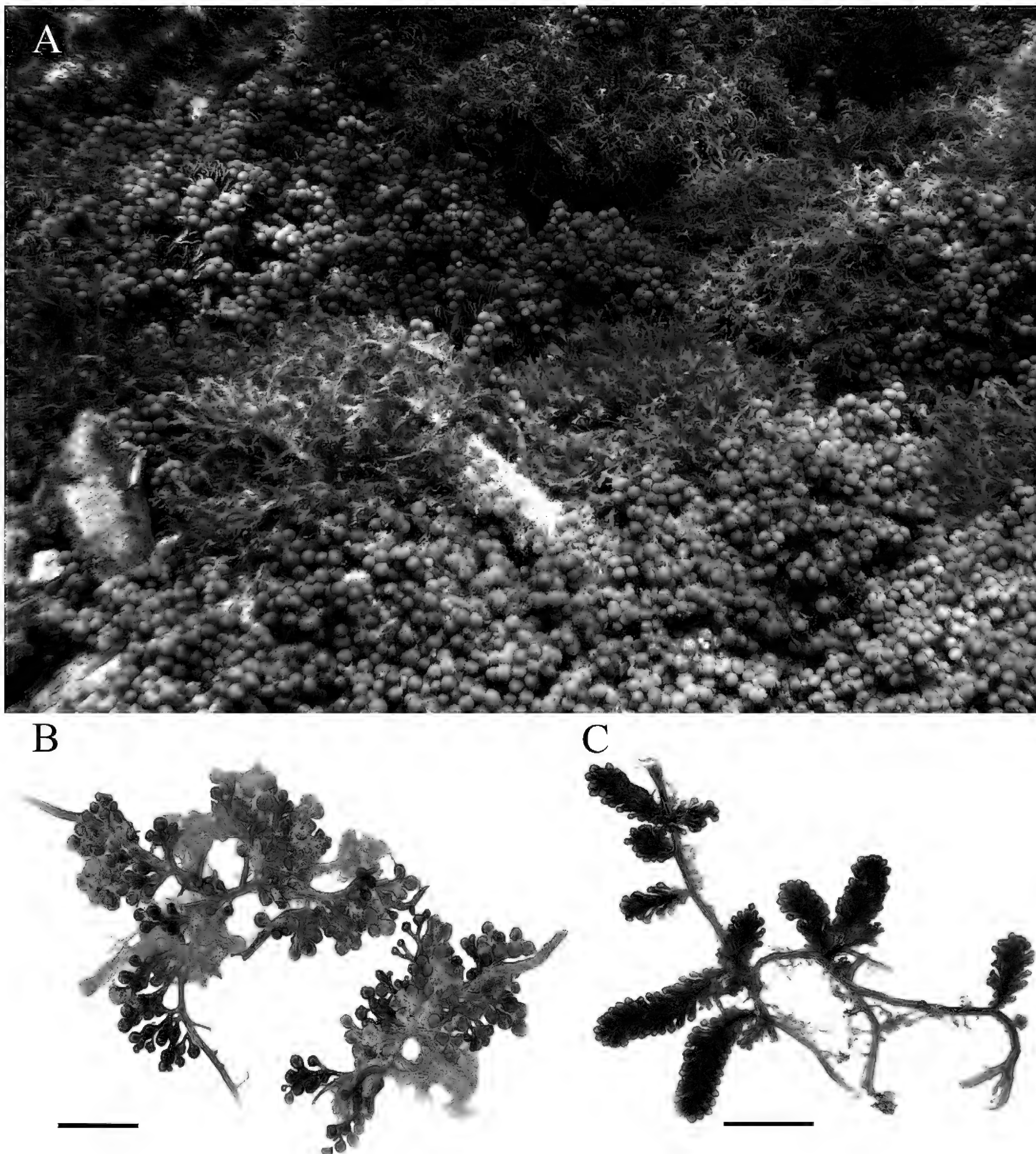


FIGURE 17. *Caulerpa racemosa*. (A) *C. racemosa* var. *racemosa*. In situ habit photograph from Enrique Reef, 0.5 m. Field = approximately 15 cm. (B) *C. racemosa* var. *macrophysa*. LRA3023, herbarium specimen: Bahia Fosforescente, low-water mark. Scale bar = 2.0 cm. (C) *C. racemosa* var. *uvifera*. DLB1485, herbarium specimen: Ballena Bay, Guánica, 2.0 m. Scale bar = 2.0 cm.



***Caulerpa racemosa* var. *uvifera* (C. Agardh)  
J. Agardh**

FIGURE 17C

*Caulerpa racemosa* var. *uvifera* (C. Agardh) J. Agardh 1873: 35.

*Basionym*: *Caulerpa uvifera* C. Agardh 1817: xxiii.

*Puerto Rican Record*: Almodóvar 1962.

*Western Atlantic Distribution*: North America, Bermuda, Puerto Rico, Trinidad and Tobago, Brazil.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Red Sea.

Terete assimilators are erect, imbricate, and mostly up to 2.5 cm tall and bear densely crowded branchlets with short, up to 3 mm long, stalks that are distally swollen, with a compressed to flattened summit, 1.5–2.5 mm diam.

*Habitat and Comments*: *Caulerpa racemosa* var. *uvifera* occurs in shallow waters on rocks, reefs, and sandy sediment in Puerto Rico. Some (e.g., Wynne 2005; Dawes and Mathieson 2008) have treated *C. racemosa* var. *uvifera* as a synonym of *C. racemosa*, and in their analyses Belton et al. (2014: 50) concluded *C. uvifera* C. Agardh (1817) is a heterotypic synonym of *C. racemosa*. Nevertheless, as with *Caulerpa chemnitzia*, we recognize the descriptive value of stable morphological expressions, and in this treatment, we list the variety. [Additional illustrations: as *C. uvifera*, Svedelius 1906: fig. 15; as *C. racemosa*, Taylor 1960: pl. 17: fig. 3, pl. 18: fig. 4.]

***Caulerpa serrulata* (Forssk.) J. Agardh**

FIGURE 18

*Caulerpa serrulata* (Forssk.) J. Agardh 1837: 174.

*Basionym*: *Fucus serrulatus* Forssk. 1775: 189.

*Puerto Rican Records*: As *Caulerpa serrulata*: Almodóvar and Ballantine 1983; Ruiz and Ballantine 2009; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution*: Belize, Costa Rica, Panama, Bahamas, Barbados, Cuba, Grenadines, Guadeloupe, Martinique, Netherlands Antilles, Puerto Rico, St. Eustatius, St. Barthélemy, Trinidad and Tobago, Brazil, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Mokha (=Al-Mukhā, Mocha), Yemen, Red Sea.

Assimilators are erect, up to 4.0 cm tall, with a terete to slightly compressed stipe-like lower portion that becomes compressed to a nearly flat blade that is mostly dichotomously branched (or occasionally unbranched). The blades are 2.0–4.0 mm wide, 2.0–3.5 cm long, and 1.5–2.5 mm thick. Characteristically, the branches are spirally twisted and have serrate margins with mucronate teeth, to 1.5 mm diam and 1.0 mm long. Rhizomes, 1.0–2.0 mm diam, are firmly attached to the substratum and bear slender, branching rhizoid-like filaments.

*Habit and Comments*: Although not common in Puerto Rico, *Caulerpa serrulata* can be found in shallow water in sandy habitats. [Additional illustrations: Taylor 1960: pl. 14: fig. 5; Littler and Littler 2000: 373; Braune and Guiry 2011: fig. 18.14.]

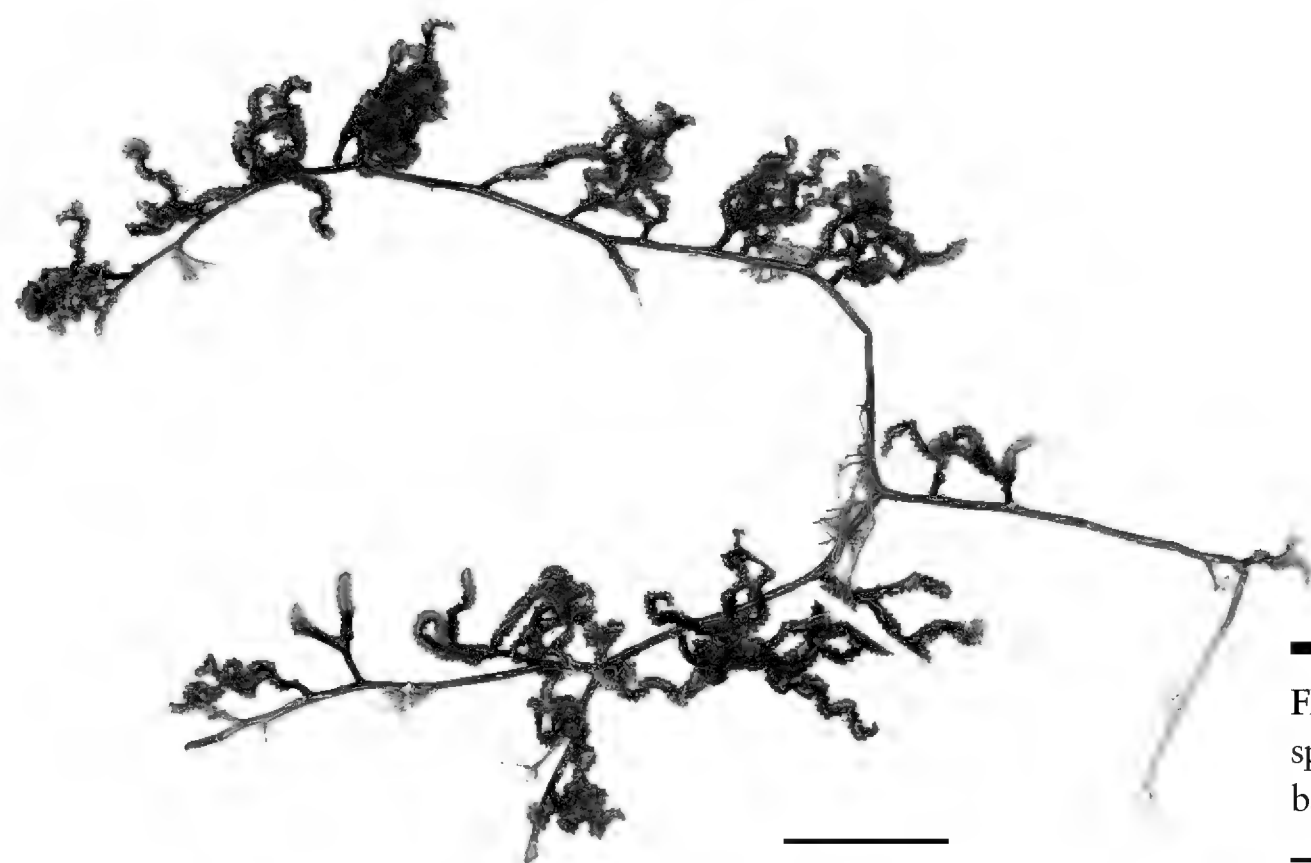


FIGURE 18. *Caulerpa serrulata*. DLB1700, herbarium specimen: Caracoles Reef, La Parguera, 6.0 m. Scale bar = 2.0 cm.

***Caulerpa sertularioides* (S. G. Gmelin)  
M. Howe f. *sertularioides***

FIGURE 19A

*Caulerpa sertularioides* (S. G. Gmelin) M. Howe 1905: 576.  
*Basionym*: *Fucus sertularioides* S. G. Gmelin 1768: 151, pl. 15, fig. 4.  
*Heterotypic Synonym*: *Caulerpa plumaris* (Forssk.) C. Agardh 1823: 436.

*Puerto Rican Records*: As *Caulerpa sertularioides*: Howe 1915; Taylor 1960; Almodóvar 1964a, 1964b, 1971; Almodóvar and Pagán 1971; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution*: Belize, Costa Rica, Nicaragua, Panama, Veracruz, North America, Bermuda, Bahamas, Barbados, Bequia, Cayman Islands, Antigua, Dominica, Grenadines, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Nevis, Puerto Rico, St. Eustatius, St. Lucia, Trinidad and Tobago, Brazil, Colombia, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: “In coralliis americanis” (Gmelin 1768); tropical America (Lipkin and Silva 2002).

Thalli possess extensive systems of coarse rhizomes, to 2.0 m in extent and 2.2–5.0 mm diam. Assimilators are to 20 cm tall and 1.0–1.5 mm diam, with 2(–3 or more) ranks of distichous branchlets. The typical form possesses opposite branching, giving the entire plant a feather-like appearance. Branchlets are cylindrical, 10–15 mm long and 180–330 µm diam, terminating in acute tips.

*Habitat and Comments*: *Caulerpa sertularioides* occurs in shallow-water mangrove habitats on *Rhizophora* prop roots as well as beneath them and in seagrass beds. In Puerto Rico, *C. sertularioides* can also be found at offshore algal plains down to 24 m depths. Leichter et al. (2008) reported the species in the Florida Keys at depths of 40–60 m. [Additional illustrations: as *Caulerpa plumaris*, Harvey 1858: pl. 38C; as *Caulerpa sertularioides*, Littler et al. 2008: 222.]

***Caulerpa sertularioides* f. *brevipes* (J. Agardh) Sved.**

FIGURE 19B

*Caulerpa sertularioides* f. *brevipes* (J. Agardh) Sved. 1906: 114, figs. 7, 8.  
*Basionym*: *Caulerpa plumaris* var. *brevipes* J. Agardh 1873: 15.

*Puerto Rican Records*: As *Caulerpa sertularioides* f. *brevipes*: Almodóvar 1962; Almodóvar and Blomquist 1959.

*Western Atlantic Distribution*: Costa Rica, Mexico, Panama, North America, Bermuda, Bahamas, Antigua, Barbados, Cuba, Dominica, Grenadines, Netherlands Antilles, Puerto Rico, St. Kitts, U.S. Virgin Islands, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Syntype Localities*: West Indies, Pacific Ocean, Sri Lanka, and Red Sea (Silva et al. 1996).

Thalli are erect, short, only 1.0–5.0 cm tall, with sessile or rarely forked, feather-like assimilators.

*Habitat and Comments*: *Caulerpa sertularioides* f. *brevipes* often forms colonies on hard substrata or reef environments in partially exposed habitats in shallow waters. [Additional illustrations: Svedelius 1906: figs. 7, 8; Taylor 1960: pl. 13: figs. 2, 3.]

***Caulerpa sertularioides* f. *farlowii* (Weber Bosse)  
Børgesen**

FIGURE 19D

*Caulerpa sertularioides* f. *farlowii* (Weber Bosse) Børgesen 1907: 365, fig. 11.  
*Basionym*: *Caulerpa plumaris* f. *farlowii* Weber Bosse 1898: 295, pl. 24, figs. 5, 6.

*Puerto Rican Records*: Almodóvar 1962; Ballantine 1977.

*Western Atlantic Distribution*: Belize, Costa Rica, North America, Cuba, Netherlands Antilles, Puerto Rico, Venezuela

*World Distribution*: See Guiry and Guiry (2022).

*Syntype Localities*: Florida, USA; Ilhas do Cabo Verde; and Flores Island, Lesser Sunda Islands, Indonesia (Silva et al. 1996).

Thalli are erect, 5.0–10 cm tall, with axes that are densely crowded with radially arranged, cylindrical branchlets, 5.0–8.0 mm long and 500–700 µm diam. The creeping rhizomes measure 2.0–5.0 mm diam.

*Habitat and Comments*: *Caulerpa sertularioides* f. *farlowii*, in contrast to the other feather-like varieties and forms of *C. sertularioides*, is somewhat rounded and brush-like in appearance. It generally occurs in sandy areas of reef flats and shallow-water sandy habitats down to 8.0 m depths. [Additional illustrations: Taylor 1960: pl. 13: figs. 4, 5; Littler and Littler 2000: 375.]

***Caulerpa sertularioides* f. *longiseta* (Bory) Sved.**

FIGURE 19C

*Caulerpa sertularioides* f. *longiseta* (Bory) Sved. 1906: 114, fig. 10.  
*Basionym*: *Caulerpa plumaris* var. *longiseta* Bory 1828: 194, pl. 22, fig. 4.

*Puerto Rican Record*: Almodóvar 1962.

*Western Atlantic Distribution*: Panama, Costa Rica, North America, Bermuda, Cuba, Martinique, Puerto Rico, Brazil, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Not specified (Silva et al. 1996).

Thalli are erect and up to 20 cm tall, with assimilators that are subdichotomously to dichotomously 2–4 times branched. This taxon has a distinctive feather-like appearance, bearing long, opposite branchlets in 2 ranks, 2.0–5.0 mm long and 300–500 µm diam. Rhizomes are up to 1.0 m in extent and 1.8–2.2 mm diam.

*Habitat and Comments*: *Caulerpa sertularioides* f. *longiseta* occurs in shallow-water sandy areas and seagrass beds down to 10 m depths. Sauvage et al. (2021) pointed out the remarkable morphological similarity between this forma and the “plumose” morphology of *Caulerpa wysorii* T. Sauvage et M. J. Wynne. [Additional illustrations: Svedelius 1906: fig. 10; Taylor 1960: pl. 13: figs. 6, 7; Littler and Littler 1997: 375.]

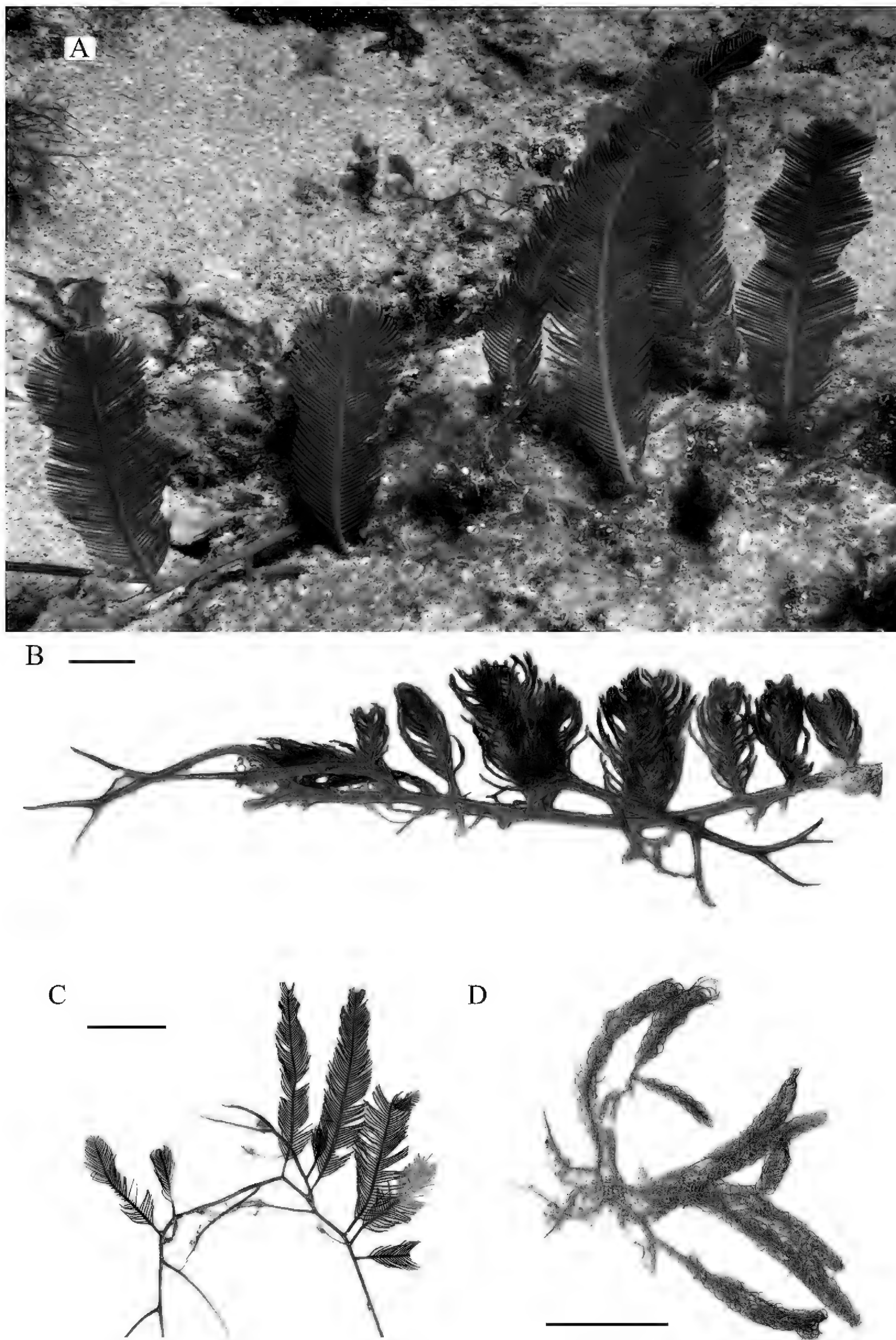


FIGURE 19. *Caulerpa sertularioides*. (A). *C. sertularioides* f. *sertularioides*. In situ habit photograph from algal plain, seaward Media Luna Reef, 17 m. Field = approximately 15 cm. (B) *C. sertularioides* f. *brevipes*. MDP59: Puerto Real. Scale bar = 1.0 cm. (C) *C. sertularioides* f. *longiseta*. DLBsn: Ensenada Honda, Cul-ebra Island, epiphytic on *Rhizophora mangle*. Scale bar = 1.0 cm. (D) *C. sertularioides* f. *farlowii*. DLB384: Algal plain, seaward, Media Luna Reef, 17 m. Scale bar = 1.0 cm.

## ***Caulerpa taxifolia* (M. Vahl) C. Agardh**

FIGURE 20

*Caulerpa taxifolia* (H. West in M. Vahl) C. Agardh 1817: xxii.  
*Basionym*: *Fucus taxifolius* H. West in M. Vahl 1802: 36.

*Puerto Rican Records*: As *Caulerpa taxifolia*: Howe 1915; Almodóvar and Blomquist 1959, 1961; Taylor 1960; Almodóvar 1962, 1964a, 1964b; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution*: Belize, Mexico, Panama, North America, Bermuda, Antigua, Barbados, Dominica, Grenadines, Jamaica, Martinique, Netherlands Antilles, Nevis, Puerto Rico, St. Kitts, St. Lucia, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: St. Croix, U.S. Virgin Islands.

Thalli are to 15 cm tall with slightly compressed assimilators, 1.0–1.5 mm diam, that produce opposite pinnate branchlets that are constricted at their bases. The branchlets, 0.6–1.0 mm wide and to 6.0 mm long, are strongly compressed and upcurved. Branchlets are slightly constricted where cut off from the assimilators and are tapered both proximally and distally.

*Habitat and Comments*: In Puerto Rico *Caulerpa taxifolia* is common in mangrove habitats among *Rhizophora* roots and offshore in sandy habitats of reefs down to a depth of 30 m. It is sometimes difficult to separate *C. taxifolia* from

the similar-looking *C. mexicana*. *Caulerpa taxifolia* possesses strongly compressed branchlets that are constricted at their base, whereas *C. mexicana* has broad, flat branchlets not constricted at their base.

As an invasive species, *C. taxifolia* has achieved a great deal of notoriety following its introduction, presumably escaping from the Oceanographic Museum in Monaco, and has spread into the Mediterranean Sea, where it has been responsible for displacing native species (e.g., Santini-Bellan et al. 1996; Jousson et al. 1998; Meinesz 1999; Guiry and Guiry 2022). [Additional illustrations: Yamada 1934: figs. 36, 37; Littler and Littler 2000: 377; Braune and Guiry 2011: fig. 18.16.]

## ***Caulerpa webbiana* Mont.**

FIGURE 21

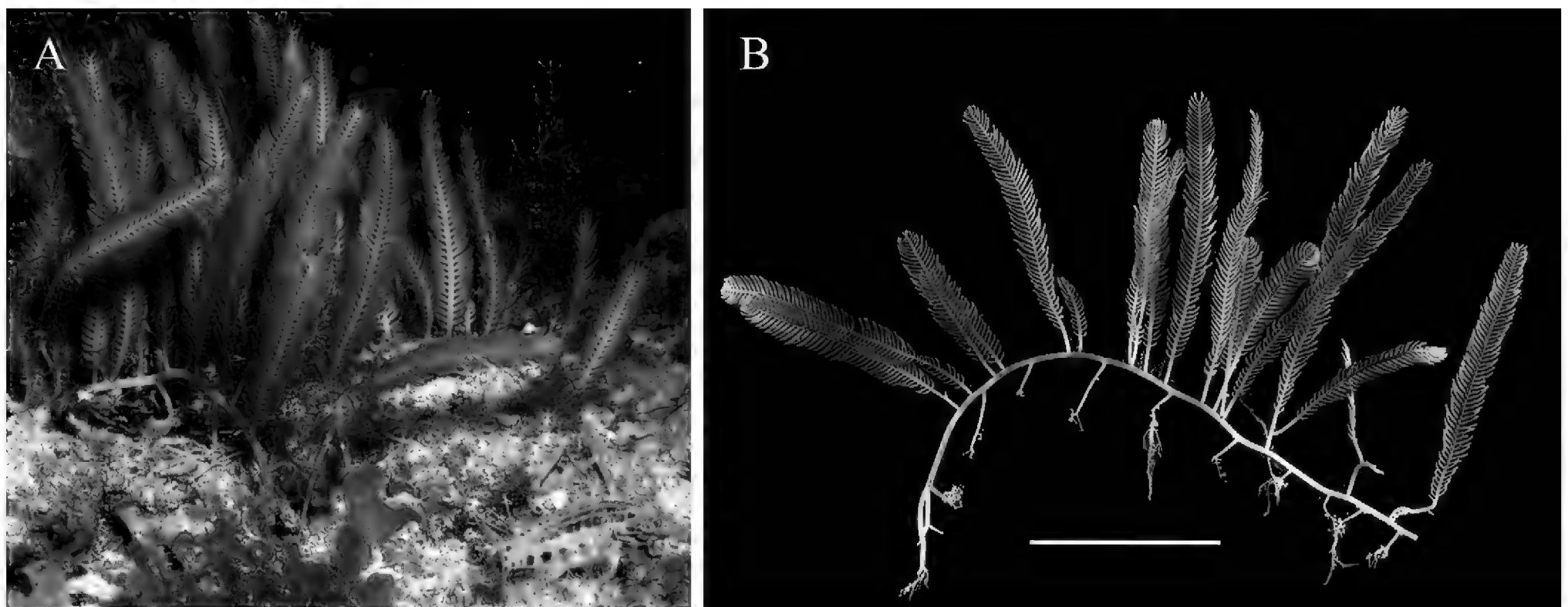
*Caulerpa webbiana* Mont. 1837: 429 [misprinted as p. 529].

*Puerto Rican Records*: Taylor 1960; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution*: Costa Rica, North America, Barbados, Guadeloupe, Jamaica, Puerto Rico, St. Kitts, U.S. Virgin Islands, Brazil.

*Other Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Arrecife, Isla Lanzarote, Canary Island, Spain.



**FIGURE 20.** *Caulerpa taxifolia*. (A) In situ habit photograph from algal plain, seaward of Media Luna Reef, 17 m. Note lantern basslet, *Serranus baldwini* (Evermann et Marsh) in foreground. Field = approximately 10 cm. (B) Detail of plant assimilator with branchlets. Scale bar = 5.0 cm.



Erect algae are small and inconspicuous to mat forming, up to 15 mm tall, with terete assimilators that bear sometimes indistinct whorls of 2–6 determinate branchlets. Branchlets are dichotomously branched 3–5 times and about 250  $\mu\text{m}$  in length, with a terete base that flattens distally where it bears 1–2 furcate or mucronate apices. The creeping rhizomes measure up to 400  $\mu\text{m}$  diam. Both the rhizomes and older assimilators are sparsely to densely covered with rhizoids. Algae are yellow green in color.

**Habitat and Comments:** Apparently rare in Puerto Rico, *Caulerpa webbiana* occurs in sandy habitats and algal plains with coral fragments and rubble. Taylor (1960) noted that the species occurs from the intertidal down to depths of 50 m, and recently, Ballantine et al. (2016) found *C. webbiana* in Puerto Rico down to 100 m depths. [Additional illustrations: Vickers 1908: pl. 39: figs. 1–8; Taylor 1960: pl. 10: fig. 10.]

### ***Caulerpa wysorii* T. Sauvage et M. J. Wynne**

FIGURE 22

*Caulerpa wysorii* T. Sauvage et M. J. Wynne in Sauvage et al. 2021: 117, figs. 3, 4, 13.

**Puerto Rican Records:** Newly reported herein from Puerto Rico: DLB1360, algal plain, seaward Margarita Reef, La Parguera, 24 m (17.IX.1983); DLB1489, algal plain, seaward Margarita Reef, La Parguera, 24 m (18.X.1983); DLB2778, algal plain, seaward Media Luna Reef, La Parguera, 17 m (10.III.1987).

**Western Atlantic Distribution:** Mexico, North America, Puerto Rico.

**Type Locality:** Florida Middle Grounds, NE Gulf of Mexico.

Thalli possess two distinct morphologies. Specimens of the “plumose” morphology produce assimilators to 12 cm in height. These produce opposite branchlets, 1.0–1.5 cm long and less than 1.0 mm diam. The branchlets possess acute apices. Specimens of the “filiform” morphology possess assimilators to 20 cm tall and 1.0–2.0 mm diam. These assimilators have few dichotomous or subdichotomous branches and do not possess branchlets. Algae are olive green in culture.

**Habitat and Comments:** In Puerto Rico, *C. wysorii* is known only from two south coast, offshore algal plains at 17 and 24 m depths. All Puerto Rican plants are of the filiform morphology. The taxon has a very simple morphology, producing assimilators to 15 cm tall from an elongate rhizome. The rhizomes measure from 1.0 to 1.4 mm diam, and assimilators measure from 0.8 to 1.0 mm diam. Apices are blunt. Assimilator branching is equally or unequally dichotomous as well as unilateral. Rhizomes produce rhizoids ventrally at irregular intervals of 15 to 35 mm. The plumose morphology of *C. wysorii* bears close resemblance to *Caulerpa sertularioides* f. *longiseta*. As the plumose form of *C. wysorii* is known only from mesophotic depths, Puerto Rican *C. sertularioides* f. *longiseta* probably does not represent the plumose form of *C. wysorii*. [Additional illustration: Sauvage et al. 2014: fig. 12.]

### ***Caulerpa* subgen. *Caulerpella* (Prud’homme et Lokhorst) Draisma, Prud’homme, et T. Sauvage**

*Caulerpa* subgen. *Caulerpella* (Prud’homme et Lokhorst) Draisma, Prud’homme, et T. Sauvage in Draisma et al. 2014: 1031.

**Basionym:** *Caulerpella* Prud’homme et Lokhorst 1992.

**Type Species:** *Caulerpa ambigua* Okamura 1897: 4, pl. 1: figs. 3–12.

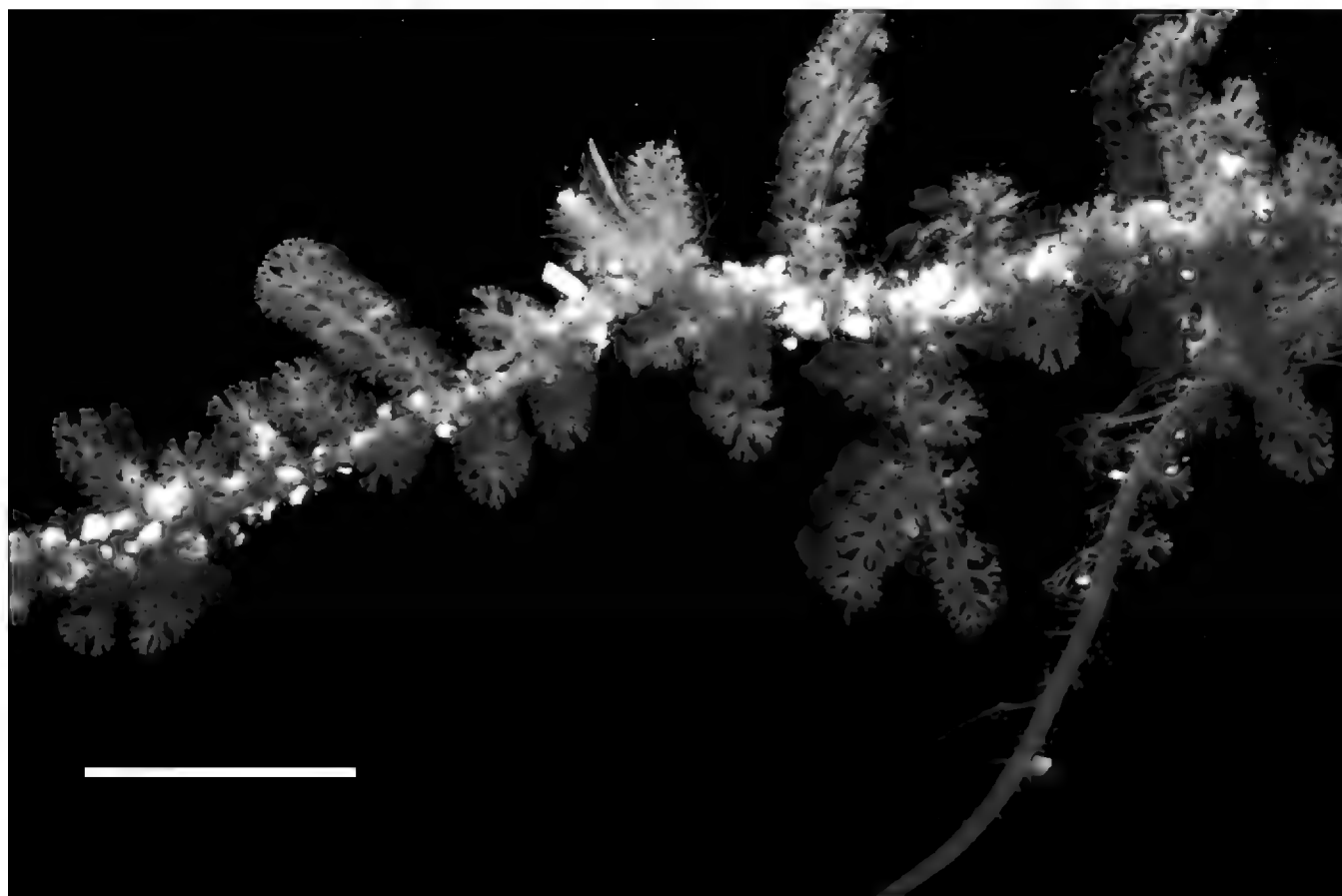


FIGURE 21. *Caulerpa webbiana*. Habit photograph from algal plain, seaward of Media Luna Reef, 17 m. Scale bar = 1.0 mm.



Species of *Caulerpa* subgen. *Caulerpella* are nonholocarpic and develop zoidangia that are separated from the vegetative part of the thallus by a cell wall.

**Comments:** Prud'homme van Reine and Lokhorst (1992) distinguished *Caulerpella* from *Caulerpa* by its nonholocarpic specialized lobed reproduction organs. Silva et al. (1996), however, retained *C. ambigua* in *Caulerpa* on the basis of the trabeculate structures it shares with the genus. Lipkin and Silva (2002) suggested that if the reproductive function of the lobed structures were confirmed, that would distinguish it from *Caulerpa*, and Draisma et al. (2014) in their molecular phylogeny concluded it to be a subgenus. Draisma et al. (2014) also suggested there is more than one taxon in *Caulerpa* subgen. *Caulerpella*.

### ***Caulerpa vickersiae* Børgesen**

FIGURE 23

*Caulerpa vickersiae* Børgesen 1911: 129, fig. 2.

**Synonym:** *Caulerpa ambigua* sensu Vickers 1908: 37.

**Misapplied Name:** Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine et al. 2016 [non *Caulerpa ambigua* Okamura 1897: 4]. *Caulerpella ambigua* sensu Ballantine and Aponte 1997a, 2002 [non *Caulerpella ambigua* (Okamura) Prud'homme et Lokhorst 1992: 11].

**Puerto Rican Records:** As *Caulerpa ambigua*: Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine et al. 2016. As *Caulerpella ambigua*: Ballantine and Aponte 1997a, 2002.

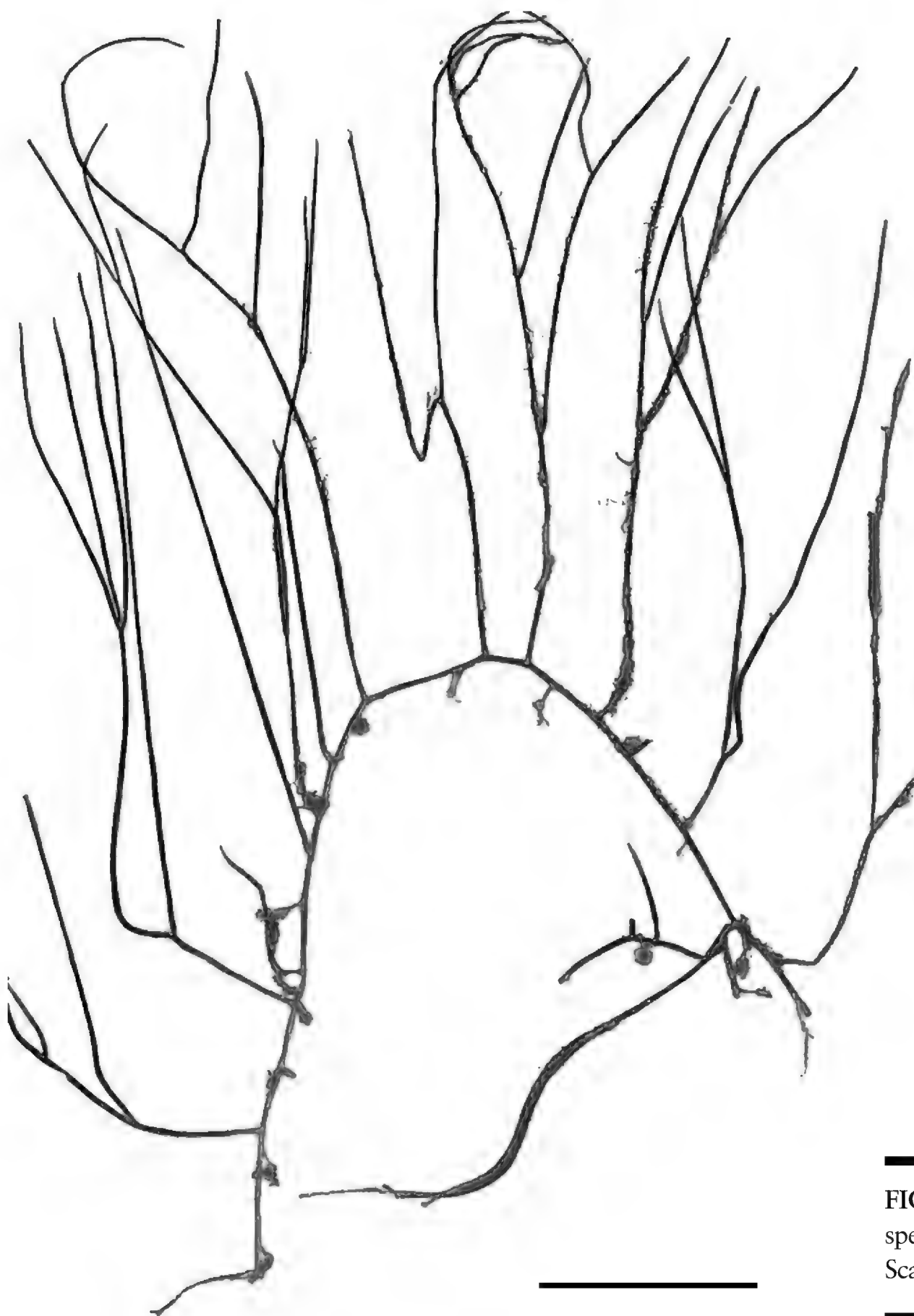


FIGURE 22. *Caulerpa wysorii*. DLB1360, herbarium specimen: Seaward Margarita Reef, La Parguera, 24 m. Scale bar = 2.0 cm.

**Western Atlantic Distribution:** Belize, Costa Rica, Panama, North America, Bermuda, Antigua, Barbados, Cuba, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, Saba, St. Barthélemy, St. Eustatius, St. Kitts, St. Lucia, St. Martin, U.S. Virgin Islands, Colombia, Brazil, Venezuela.

**World Distribution:** See Guiry and Guiry (2022).

**Syntype Localities:** St. John, U.S. Virgin Islands; Barbados (Silva et al., 1996: 813).

Thalli are very small and often inconspicuous. Assimilators are very narrow, cylindrical, and unbranched or occasionally divided, 1.0(–2.0) cm tall and 100–150  $\mu\text{m}$  diam. The lowermost portion of erect axes is a short or inconspicuous naked stalk that bears pinnately placed branchlets that are simple or occasionally forked, 60–100  $\mu\text{m}$  diam and up to 500  $\mu\text{m}$  long, with blunt tips. Stolons are slender, 200–250  $\mu\text{m}$  diam.

**Habitat and Comments:** *Caulerpa vickersiae* occurs on dead coral and fragments on reefs. Despite being inconspicuous because of its small size, the species is common at the Puerto Rican shelf edge and into deeper waters to a depth of 40 m (Ballantine et al. 2016).

There is some disagreement as to the status of Caribbean *Caulerpa vickersiae* and *Caulerpa ambigua*. Wynne (2017) and Guiry and Guiry (2022) treated the taxon as *Caulerpa ambigua*. Nevertheless, Børgesen (1911) concluded that his West Indian *Caulerpa vickersiae* was in agreement with Vickers (1908: pl. 37: figs. 3–6, as *C. ambigua*), and similar to, but unlike, two of the figures of *C. ambigua* illustrated by Okamura (1897: pl. 1: figs. 9, 10). Those figures illustrate inflated branchlets that are unlike those seen in Puerto Rican and Caribbean material. However, others have followed Børgesen and recognize *C. vickersiae* and *C. ambigua* as two separate species (e.g., Littler and Littler 2000; Dawes and Mathieson 2008). Until a molecular comparison between type locality material of *C. ambigua* and Caribbean *C. vickersiae* can be made, we prefer to relate the Caribbean taxon to the latter species. Earlier, Eubank (1946) treated *C. ambigua* as a variable species and concluded there were at least four varieties, including *C. ambigua* var. *vickersiae* (Børgesen) Eubank. Distinguished by its alternating series of simple and forked branchlets, it was

one of the varieties that Kraft (2007: 164, fig. 62C), as *Caulerpella ambigua* var. *vickersiae*, recognized from Lord Howe Island. *Caulerpa vickersiae* var. *furcifolia* W. R. Taylor (1933: 397, figs. 1–3) was described from Costa Rica; however, it is recognized as synonymous with the nominate species. [Additional illustrations: as *Caulerpa ambigua*, Vickers 1908: pl. 37; as *Caulerpa vickersiae*, Børgesen 1911: fig. 2; Taylor 1960: pl. 10: figs. 3–9.]

### ***Caulerpa* subgen. *Charoideae* (J. Agardh ex De Toni) Draisma, Prud'homme, T. Sauvage, et Belton**

*Caulerpa* subgen. *Charoideae* (J. Agardh ex De Toni) Draisma, Prud'homme, T. Sauvage, et G. Belton in Draisma et al. 2014: 1031.

**Basionym:** *Caulerpa* sect. *Charoideae* J. Agardh ex De Toni in De Toni 1889: 470.

**Type Species:** *Caulerpa verticillata* J. Agardh 1847: 6.

Species of *Caulerpa* subgen. *Charoideae* have thin, pubescent stolons and upper verticillate (whorled) fronds that are much branched, with thin branchlets. Chloroplasts are 3.0–5.0  $\mu\text{m}$  long, and without pyrenoids. Two species of *C. subgen. Charoideae* occur in Puerto Rico.

### ***Caulerpa pusilla* (Kütz.) J. Agardh**

*Caulerpa pusilla* (Kütz.) J. Agardh 1873: 6.

**Basionym:** *Stephanocoelium pusillum* Kütz. 1847: 54.

**Puerto Rican Records:** As *Caulerpa pusilla*: Diaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

**Western Atlantic Distribution:** Bermuda, Barbados, Cuba, Guadeloupe, Puerto Rico, Brazil, Venezuela.

**Type Locality:** Pernambuco, Brazil fide Kütz. (1849: 500).

Thalli are small, 10–25 mm tall, forming compact mats with entangled, tomentose rhizomes, 250–300  $\mu\text{m}$  in diameter. Assimilators are rhizoidiferous at the base with a few closely placed

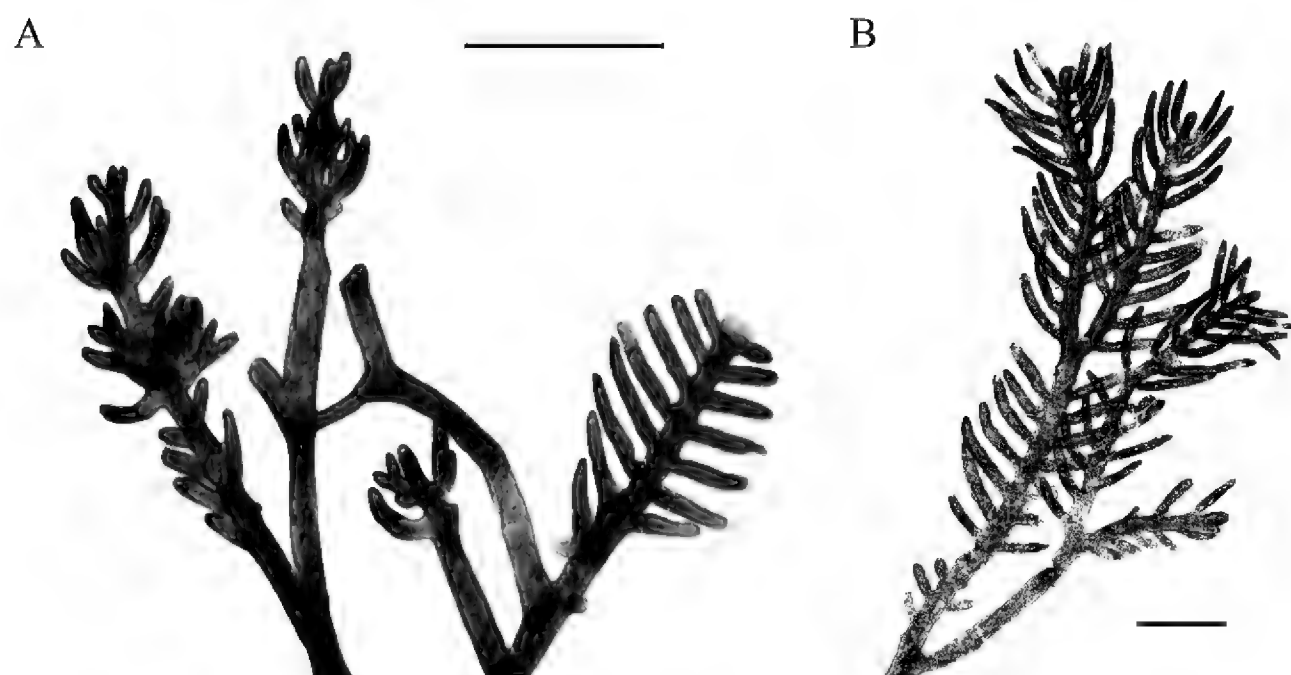


FIGURE 23. *Caulerpa vickersiae*. (A) DLB1586: Cabo Rojo lighthouse, 1.0–4.0 m. Plant with both radial and opposite branching. Scale bar = 500  $\mu\text{m}$ . (B) DLB5875, Cabo Rojo lighthouse, 0.5 m. Plant with opposite branching. Scale bar = 500  $\mu\text{m}$ .

whorls of branchlets that dichotomously branch 5–7 times and measure up to 1.5 mm diam. Whorl branchlets measure 100–140  $\mu\text{m}$  diam and are markedly constricted at the dichotomies. Each terminal segment has 2 acute tips.

*Habitat and Comments:* *Caulerpa pusilla* is inconspicuous in shallow-water habitats and algal plains of intermediate (to 40 m) depth. [Illustrations: Vickers 1908: pl. 38: figs. 1–4; Taylor 1960: pl. 10: fig. 11; Littler and Littler 2000: 369.]

### ***Caulerpa verticillata* J. Agardh**

FIGURE 24

*Caulerpa verticillata* J. Agardh 1847: 6.

*Puerto Rican Records:* Howe 1915; Almodóvar and Blomquist 1959, 1961; Taylor 1960; Almodóvar 1964a; Almodóvar and Pagán 1971; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution:* Belize, Costa Rica, Mexico, North America, Bermuda, Bahamas, Antigua, Cayman Islands, Grenadines, Guadeloupe, Hispaniola, Martinique, Netherlands Antilles, Puerto Rico, St. Eustatius, Trinidad and Tobago, Turks and Caicos Islands, U.S. Virgin Islands, Colombia, Brazil Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Not specified (Silva et al. 1996); probably West Indies (Agardh 1873).

Thalli with slender rhizomes, 300–560  $\mu\text{m}$  diam, bear erect assimilators, 1.0–3.0(–10) cm tall. The assimilators are simple or branched, bearing whorls of determinate branchlets, the entire whorl measuring 5.0–8.0 mm broad. Mucronate-tipped whorl branchlets, 100–210  $\mu\text{m}$  diam at the base and 5–10 diam long, are dichotomously branched 5–7 times. They are not constricted at the dichotomies, and branchlets decrease in diameter to 30–40  $\mu\text{m}$  diam distally.

*Habitat and Comments:* In Puerto Rico, *Caulerpa verticillata* is very common in shallow water on mangrove prop roots and moderately common on reefs and offshore algal plains at intermediate depths (10–30 m) and in deeper-water algal turfs down to 100 m (Ballantine et al. 2016). [Additional illustrations: Svedelius 1906: fig. 1; Taylor 1960: pl. 10: figs. 1, 2; Littler and Littler 2008: 223; Braune and Guiry 2011: fig. 18.18.]

### **CHAETOSIPHONACEAE F. F. BLACKMAN ET TANSLEY**

#### ***Blastophysa* Reinke**

*Blastophysa* Reinke 1889a: 87.

Thalli are minute, coenocytic cells of variable shapes, from saccate to desmid-like in shape, and commonly united by hyaline tubes in a diffuse reticulum. Chloroplasts are angular and peripheral in a sheet or network within a coenocytic cell, usually with 1 pyrenoid. Hairs are absent or infrequent. *Blastophysa*, a monotypic genus, is endophytic and epiphytic in and/or on a variety of red, brown, and green algae.

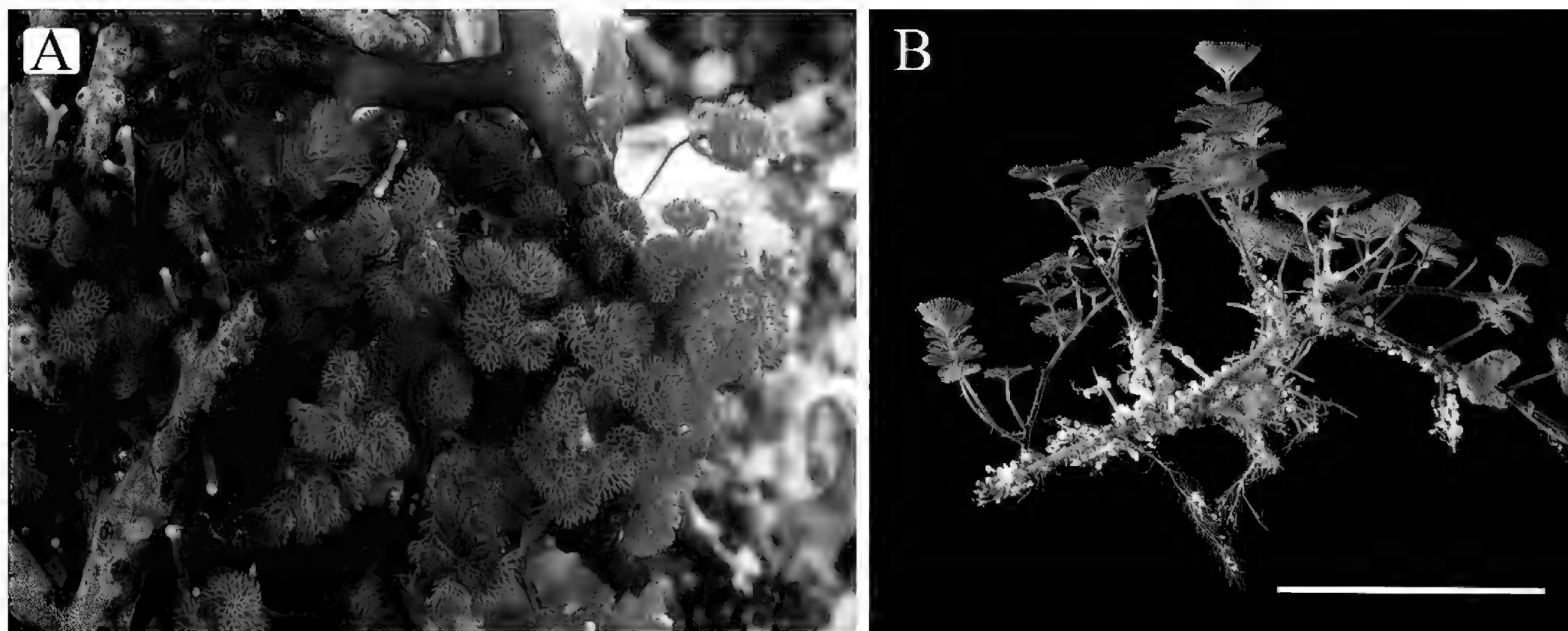


FIGURE 24. *Caulerpa verticillata*. (A) In situ habit photograph from lee of Guayacan Island, growing on *Rhizophora mangle*. Field = approximately 5.0 cm. (B) Detail of plant portion. Scale bar = 2.0 cm.

***Blastophysa rhizopus* Reinke**

*Blastophysa rhizopus* Reinke 1889a: 87, pl. 23.

*Puerto Rican Records:* Ballantine and Wynne 1986; Ballantine and Aponte 2002.

*Western Atlantic Distribution:* North America, Bermuda, Cuba, Netherlands Antilles, Puerto Rico, U.S. Virgin Islands, Brazil.

*World Distribution:* See Guiry and Guiry (2022).

*Lectotype Locality:* Kieler Förde, Kiel Bay, southwestern Baltic Sea, Germany. Note that the lectotype illustration (Reinke 1889b: pl. 23) was selected as an epitype by Burrows (1991).

*Blastophysa rhizopus* is the generitype. Thalli are microscopic coenocytic cells and grow scattered and linked by narrow, highly inconspicuous hyaline tubes within the mucilage of a red algal species. Cells are spherical, ovoid, or irregularly contoured, 25–80 µm diam, with a reticulate parietal grouping of angular chloroplasts that have a single pyrenoid surrounded by a halo of starch.

*Habitat and Comments:* In Puerto Rico, *Blastophysa rhizopus* is endophytic in *Dudresnaya* spp. and *Liagoropsis schrammi* (P. Crouan et H. Crouan) Doty et I. A. Abbott, growing in shallow and moderate depths in the vicinity of Pitahaya, La

Parguera. [Illustrations: Reinke 1889b: pl. 23; Børgesen 1911: fig. 13; Kylin 1949: fig. 63; Cormaci et al. 2014: FP389, figs. 3–5; Tsiamis et al. 2014: fig. 2A.]

**CODIACEAE KÜTZ.*****Codium* Stackh.**

*Codium* Stackh. 1797: xvi, xxiv.

Thalli are repent or erect and highly spongy in texture. Species are highly variable in habit; some are crust-like and form expanding mats, and others are upright of branched or unbranched cylindrical or flattened axes. Erect, repent, and crustose species attach to the substratum by rhizoids or rhizoidal holdfasts, and a few others are free-living or form unattached balls. Thalli are structurally composed of branching coenocytic siphons that produce a corticating layer composed of cylindrical or expanded clavate or pyriform utricles. Utricles are closely associated laterally. Chloroplasts lack pyrenoids. Gametangia are borne laterally from utricles. There are 120 species of *Codium* worldwide, of which 6 species and 1 infraspecific taxon are known from Puerto Rico.

**KEY TO THE CODIUM SPECIES OF PUERTO RICO**

1. Thalli prostrate, crust-like and lobed or repent and branched; solitary, in colonies, or forming expanding mats; attached by rhizoids ..... 2  
Thalli erect, attached by a crustose holdfast ..... 3
2. Thallus crustose, with broad, compressed lobes ..... *C. intertextum*  
Thallus forming mats, mostly cylindrical, irregularly to dichotomously divided branches, 1.0–5.0 mm in diameter ..... *C. repens*
3. Thalli with branches flattened at the dichotomies ..... 4  
Thalli with branches not flattened at the dichotomies ..... 5
4. Thalli up to 100 cm tall, branches subcylindrical and 6–25 mm in diameter; large utricles 800–2,000 µm in length ..... *C. decorticum*  
Thalli less than 15 cm tall, branches 3–4 mm in diameter ..... *C. simulans*
5. Thalli cylindrical branches, 2–6 mm in diameter, dichotomously branched; utricles 440–850 µm long ..... *C. isthmocladum*  
Branches 4–8 mm (or more) in diameter; branching unequal, frequently cervicorn; utricles 550–1,450 µm long ..... *C. taylorii*

***Codium decorticum* (Woodw.) M. Howe**

FIGURE 25

*Codium decorticum* (Woodw.) M. Howe 1911: 494.

*Basionym:* *Ulva decorticata* Woodw. 1797: 55.

*Puerto Rican Records:* As *Codium decorticum*: Diaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Belize, Costa Rica, North America, Bermuda, Guadeloupe, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Argentina, Brazil, Colombia, Uruguay, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Mediterranean Sea.

Thalli are erect, 12 cm to 1.0 m tall, with dichotomously branched axes that are attached to the substratum by cushion-like holdfasts. Branches are 6.0–25 mm in diameter and characteristically are flattened or compressed at the dichotomies.



Utricles are cylindrical, (800–) 1,100–1,750(–2,000)  $\mu\text{m}$  long and 150–850  $\mu\text{m}$  diam, with thin apical walls, 4.0–8.0  $\mu\text{m}$  in thickness. Algae are dark green in color.

*Habitat and Comments:* *Codium decorticatum* occurs in coral reef habitats from the lower intertidal and shallow water down to 15 m depths. Leichter et al. (2008) also reported that the species is found at depths of 40–60 m in the Florida Keys. [Additional illustrations: Littler et al. 2008: 211; Oliveira-Carvalho et al. 2010: figs. 2–9.]

*Puerto Rican Records:* Silva 1960; Taylor 1960; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Belize, Panama, North America, Bermuda, Barbados, Cuba, Bahamas, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherland Antilles, Puerto Rico, St. Kitts, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Tucker's Town (near mouth of Castle Harbor), St. George's Parish, Bermuda.

### ***Codium intertextum* Collins et Herv.**

FIGURE 26

*Codium intertextum* Collins et Herv. 1917: 54.

Thalli are prostrate and firm in texture, with overlapping repent lobes, up to 6.0 cm thick and to several centimeters in width. Lobes are formed above an expanding tightly adherent base (except along the margins) that is attached to the substratum by rhizoids. Peripheral utricles are cylindrical and more or less constricted

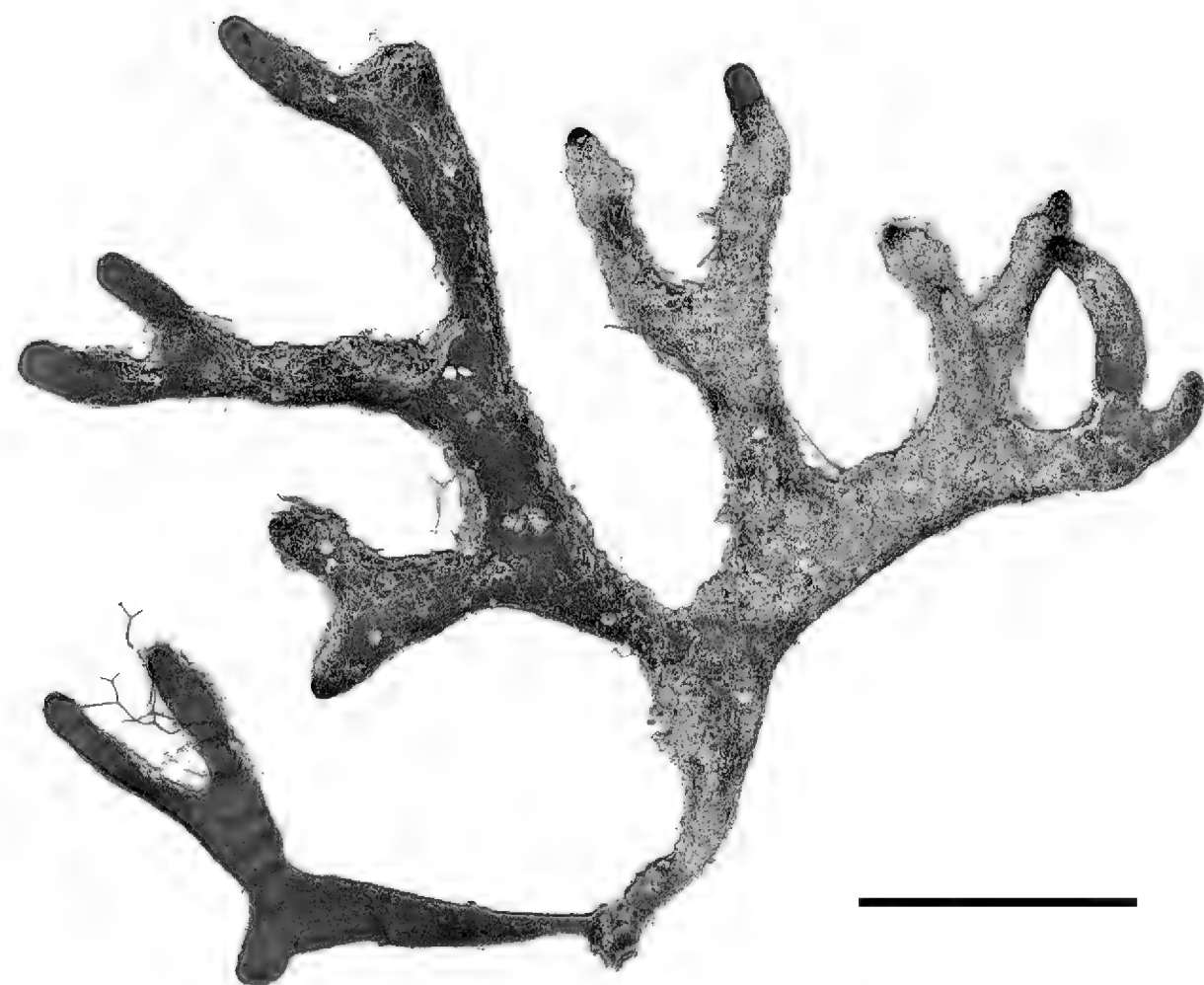


FIGURE 25. *Codium decorticatum*. DLBsn: Algal plain, seaward Media Luna reef, La Parguera, 17 m. Scale bar = 2.0 cm.

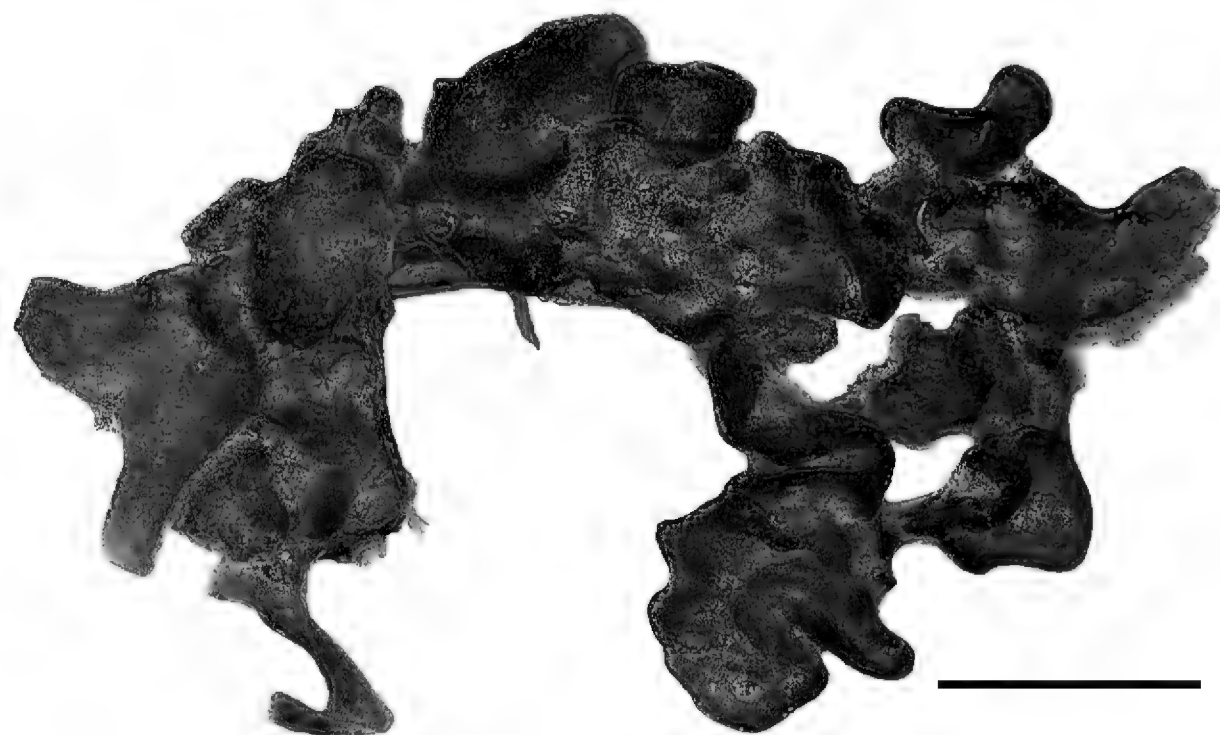


FIGURE 26. *Codium intertextum*. DLB1438: Exposed beach rock, Esperanza Beach, Manati. Scale bar = 2.0 cm.



below the apices, (45–)70–110(–215)  $\mu\text{m}$  diam and (400–)480–720(–880)  $\mu\text{m}$  long, with rounded or truncate apices and end walls 3.0–8.0(–20)  $\mu\text{m}$  thick. Algae are dull green in color.

**Habitat and Comments:** *Codium intertextum* is solitary or commonly in extensive colonies and occurs in shallow, lower intertidal waters and subtidally down to 20 m depths. [Additional illustrations: Littler et al. 2008: 212; Oliveira-Carvalho et al. 2010: figs. 10–16; Braune and Guiry 2011: fig. 19.7.]

### ***Codium isthmocladum* Vickers**

FIGURE 27

*Codium isthmocladum* Vickers 1905: 57.

*Heterotypic Synonym:* *Codium pilgeri* O. C. Schmidt 1923: 44, figs. 25, 26.

**Puerto Rican Records:** As *Codium pilgeri*: Schmidt 1923. As *Codium isthmocladum*: Silva 1960; Almodóvar and Blomquist 1961; Almodóvar 1962, 1964b; Almodóvar and Rehm 1971; Ballantine 1977, 1979; Ballantine and Aponte 2002.

**Western Atlantic Distribution:** Belize, Costa Rica, Guatemala, Panama, North America, Bermuda, Bahamas, Antigua, Barbados, Cuba, Dominica, Grenadines, Guadeloupe, Hispaniola, Honduras, Jamaica, Martinique, Netherlands Antilles, Nevis, Puerto Rico, St. Lucia, St. Martin, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Bath Beach, St. John Parish, Barbados.

**Neotype Locality:** Conset Bay, Barbados (Silva 1960: 507).

Thalli are erect, bush-like clumps, up to 20 cm tall, of dichotomously branched, terete axes and branches borne by a spongy crustose base attached to the substratum. Branches, 2.0–8.0 mm diam, are generally not flattened below dichotomies. Peripheral utricles are subcylindrical or more commonly clavate to pyriform, 120–350(–475)  $\mu\text{m}$  diam and 440–850  $\mu\text{m}$  long, with thin lateral walls (1.5  $\mu\text{m}$  thick) and thick, rounded or truncate end walls, 18–56(–110)  $\mu\text{m}$  thick. Utricles often have a constriction 130–260  $\mu\text{m}$  below the end wall. Algae are light to dark green in color.

**Habitat and Comments:** *Codium isthmocladum* occurs on reefs and under ledges in tide pools and the low intertidal. Silva (1960) observed that *C. isthmocladum* subsp. *isthmocladum* specimens from Guánica grew in the intertidal, whereas those of *C. isthmocladum* subsp. *clavatum* grew at 50 m depths. Almodóvar and Rehm (1971) reported that *C. isthmocladum* formed unattached balls in the lee of Collado Reef, La Parguera. It is of interest that *C. pilgeri* O. C. Schmidt (1923), placed in synonymy with *Codium isthmocladum* by Silva (1960), is based on a specimen collected in 1887 at Manatí by P. Sintenis. The *C. pilgeri* holotype was destroyed by fire at the Berlin Botanic Museum in 1943. [Additional illustrations: Vickers 1908: pl. 28; Silva 1960: pl. 108a, pl. 110 (type illustration), pl. 115a–f (type illustration), 503, pl. 115b (neotype illustration); Littler and Littler 2008: 213; Oliveira-Carvalho et al. 2010: figs. 17–26.]



FIGURE 27. *Codium isthmocladum*. In situ habit photograph from algal plain, seaward of Media Luna Reef, 17 m. Field = approximately 10 cm.

### ***Codium simulans* Setchell et N. L. Gardner 1924**

*Codium simulans* Setchell et N. L. Gardner 1924: 706, pl. 14: figs. 21, 22, pl. 31.

*Puerto Rican Records:* As *Codium isthmocladum* subsp. *clavatum*: Silva 1960; Ballantine et al. 2016.

*Western Atlantic Distribution:* North America, Bahamas, Bermuda, Puerto Rico, Brazil.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* San Marcos Island, Gulf of California.

Dichotomously branched thalli measure to 13 cm tall and 3.0–4.0 mm diam. Branches are cylindrical and flattened at the dichotomies. Peripheral utricles are subcylindrical to clavate, 200 µm diam distally and 600–700 µm long, with thick, rounded end walls, to 50 µm thick. Several hairs are cut off beneath the terminal wall. Gametangia are blunt and measure 100 µm diam and to 250 µm long.

*Codium isthmocladum* subsp. *clavatum* differs from *C. isthmocladum* subsp. *isthmocladum* in often having flattened and wider lower branches, 5.0–10 mm in width, and peripheral utricles that have thinner end walls.

*Habitat and Comments:* Although occurring in shallow waters, *Codium simulans* subsp. *clavatum* is common on subtidal off-shore reefs and banks in Puerto Rico. Silva (1960) noted specimens, as *Codium isthmocladum* subsp. *clavatum*, from Guánica grew at 50 m depths, and Ballantine et al. (2016) reported the species on offshore coral reef habitats at 36–60 m depths. In the Bahamas, *C. similans* (as subsp. *clavatum*) is reported from 67–73 m depths (Norris and Olsen 1991), and in Brazil it is reported at 75 m depths (Joly and Yoneshigue Braga 1966). Schneider et al. (2020) demonstrated that Bermudan species historically treated as *Codium isthmocladum* subsp. *clavatum* molecularly conformed to *Codium simulans* from Pacific Mexico. *Codium simulans* is now considered to be both a morphologically (Pedroche et al. 2002) and genetically (Schneider et al. 2020) variable species. [Illustrations: as *Codium isthmocladum* subsp. *clavatum*, Silva 1960: pls. 111a,b, 116a,b; as *C. simulans*, Schneider et al. 2020: fig. 2.]

### ***Codium repens* P. Crouan et H. Crouan**

FIGURE 28

*Codium repens* P. Crouan et H. Crouan in Vickers 1905: 56.

*Heterotypic Synonym:* *Codium tomentosum* var. *subsimplex* P. Crouan et H. Crouan in Schramm and Mazé 1865: 47.

*Puerto Rican Records:* Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Belize, Panama, North America, Bermuda, Barbados, Cuba, Guadeloupe, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, Brazil, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Vieux-Fort, Guadeloupe, French West Indies.

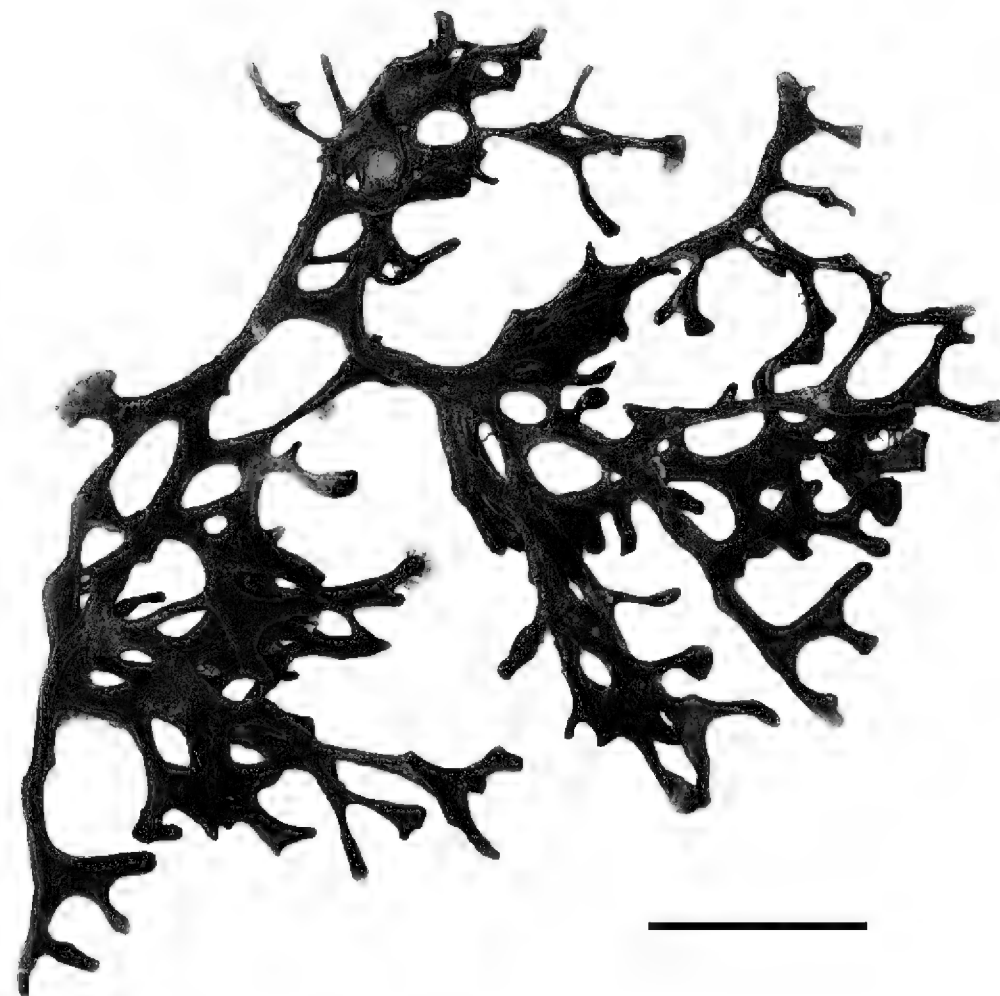


FIGURE 28. *Codium repens*. MDP3644: Cayo Caracoles, La Parguera. Scale bar = 2.0 cm.

Thalli are decumbent and irregularly to dichotomously branched, with slender terete to slightly compressed branches, 1.0–5.0 mm diam. Algae are sometimes anastomosing to form extensive mats to 40 cm in extent, frequently with secondary attachments of tufts of rhizoids. Peripheral utricles are subspherical to pyriform, 100–275 µm diam. And 330–550(–875) µm long. Utricle end walls are 4.0–6.0(–16) µm thick, with rounded or slightly flattened apices, and commonly with utricle hairs and scars. Algae are light green in color.

*Habitat and Comments:* *Codium repens* occurs on rocks, on reefs, under ledges, and in tide pools in shallow water from the intertidal to 55 m depths. In naming the species, Vickers (1905: 57) cited “Crouan mscr. in herb.” and quoted their description of *C. tomentosum* var. *subsimplex* in Schramm and Mazé (1865); thus, it is the basis and type of *Codium repens*. [Additional illustrations: Vickers 1908: pl. 29; Silva 1960: pls. 113a–e, 122a,b, 123a,b; Oliveira-Carvalho et al. 2010: figs. 33–36.]

### ***Codium taylorii* P. C. Silva**

FIGURE 29

*Codium taylorii* P. C. Silva 1960: 510, pls. 112a,b (type),c, 118b, 119a,b, 120a,b.

*Heterotypic Synonym:* *Codium abbreviatum* C. Agardh in Mazé and Schramm 1878, “nomen subnudum.”

*Puerto Rican Records:* Silva 1960; Taylor 1960; Almodóvar and Rehm 1971; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution:* Belize, Mexico, North America, Bermuda, Barbados, Bequia, Cuba, Grenadines, Guadeloupe, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, Saba Island, St. Barthélemy, St. Kitts, St. Lucia, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela, Uruguay.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Pass-a-Grille Beach, Pinellas County, Florida, USA.

Thalli are erect and bushy, reaching to 10–15 cm tall. Branches are generally flattened throughout or at least distinctly flattened below the dichotomies. Branching is dense, to 7–9 orders, and dichotomies are uneven, resulting in a cervicorn appearance. Branches are (3.0–)4.0–8.0(–25) mm broad and 3.0–4.0 mm in diameter. Peripheral utricles are slender, cylindrical, clavate, or broadly spindle shaped, and highly variable in size, (57–)110–260(–380)  $\mu\text{m}$  diam and (550–)650–1,150(–1,450)  $\mu\text{m}$  long, with slightly rounded or subtruncate apices and commonly with scars and hairs, 50–105  $\mu\text{m}$  below the utricle tip. Utricle end walls are moderately thickened, up to 23  $\mu\text{m}$  thick.

*Habitat and Comments:* *Codium taylorii* occurs on rocks, on reefs, and on mangrove roots in shallow water and in deeper water down to 60 m depths. Although Taylor (1960) suggested the species was limited to shallow water, Ballantine et al. (2016) reported the species to 50 m depth in Puerto Rico.

Almodóvar and Rehm (1971) reported it forming algal balls at Collado Reef (La Parguera, Puerto Rico). [Additional illustrations: Littler et al. 2008: 214; Oliveira-Carvalho et al. 2010: figs. 48–54.]

The taxonomic status of *Codium taylorii* is somewhat questionable. The taxon *C. taylori* is preceded by *Codium abbreviatum* C. Agardh (in Mazé and Schramm 1877). Silva (1960: 510) in describing *Codium taylorii* listed *C. abbreviatum* as “*nomen subnudum*” and stated that he did not consider their reference to color as constituting valid description of this species (Silva 1960: 513).

## DERBESACEAE HAUCK

### *Derbesia* Solier

*Derbesia* Solier 1846: 458.

Thalli are usually of two different morphological forms. Sporophytic thalli consist of cylindrical, coenocytic filaments that are usually erect and loosely unilaterally, irregularly, or sometimes dichotomously branched. They are attached by rhizoidal filaments or lobed haptera. Gametophytic thalli are pyriform or spherical and saclike, single-celled vesicles. They are generally attached to crustose coralline algae by basal rhizoids. Both filamentous and vesicular forms are multinucleate,

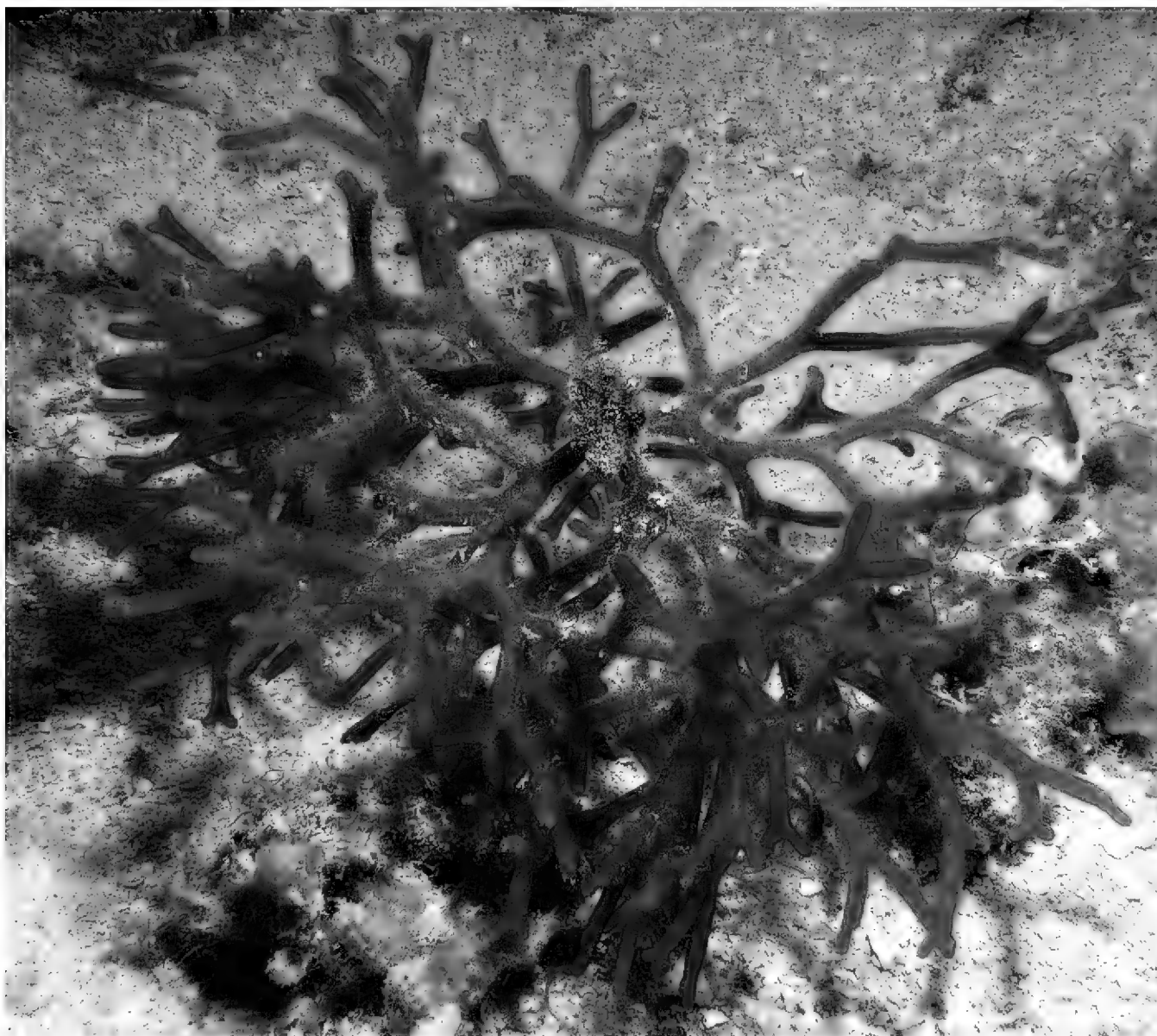


FIGURE 29. *Codium taylorii*. In situ habit photograph from algal plain, seaward of Media Luna Reef, La Parguera. Field = approximately 10 cm.



with numerous discoid or spindle-shaped chloroplasts. Some species possess 1–3 pyrenoids, and others lack pyrenoids. Asexual reproduction occurs by fragmentation or production of extruded protoplasts. The *Derbesia* phase sporophytic filaments produce zoospores in lateral sporangia separated from

the bearing vegetative filament by a single or double septum near its base. A vesicular gametophytic *Halicystis* phase is known in life histories of some *Derbesia* species. There are 19 recognized species of *Derbesia*, 2 of which occur in Puerto Rico.

#### KEY TO THE *DERBESIA* SPECIES OF PUERTO RICO

1. Thalli vesicular, spherical to pyriform, usually less than 7.0 mm diam ..... *D. osterhoutii*  
Plants filamentous, dichotomously branched, less than 50 µm diam ..... *D. vaucheriiformis*

#### ***Derbesia osterhoutii* (L. R. Blinks et A. C. H. Blinks) J. R. Z. Page**

FIGURE 30

*Derbesia osterhoutii* (L. R. Blinks et A. C. H. Blinks) J. R. Z. Page 1970: 380, figs. 1–6.

*Basionym*: *Halicystis osterhoutii* L. R. Blinks et A. C. H. Blinks 1931: 389, fig. 18, pl. 22: figs. 1–8, pl. 23: figs. 9–12.

*Puerto Rican Records*: As *Derbesia osterhoutii*: Ballantine et al. 2009, 2016.

*Western Atlantic Distribution*: North America, Bermuda, Bahamas, Grenadines, Jamaica, Puerto Rico.

*Type Locality*: Great Sound, Bermuda.

The generally solitary gametophytes are ovoid to spherical vesicles, measuring 7.0 mm to 3.0 cm diam, and are attached by

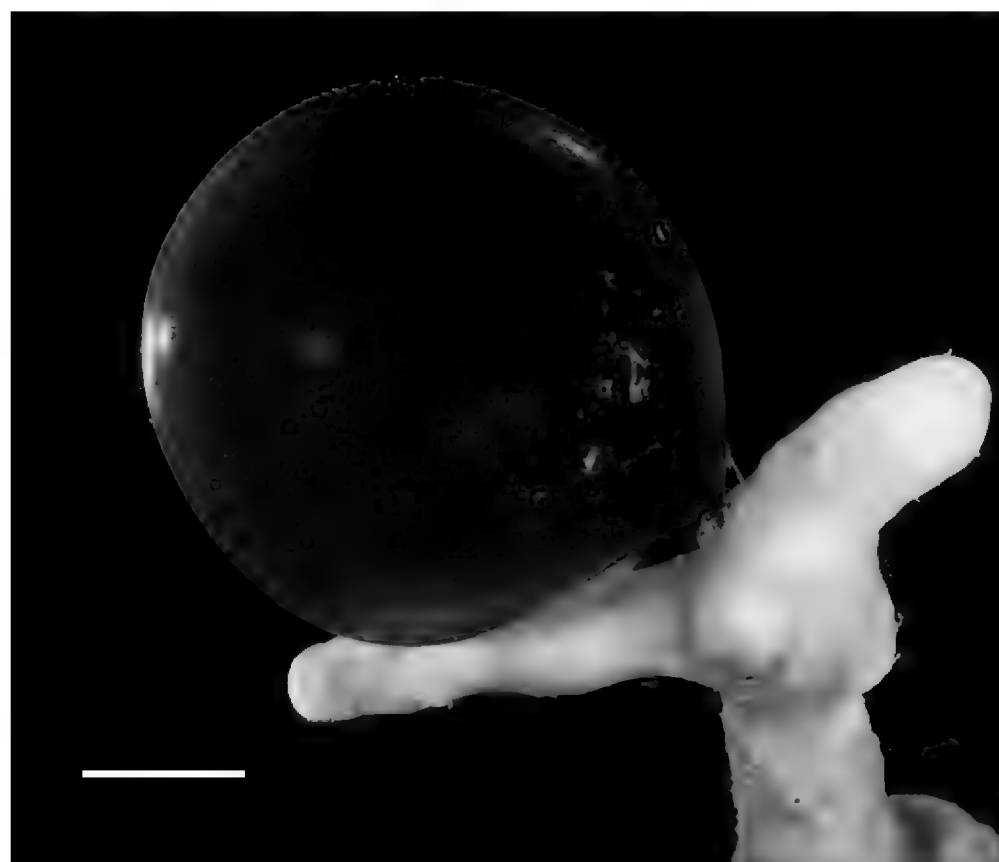


FIGURE 30. *Derbesia osterhoutii*. In situ habit photograph from edge of insular shelf offshore from La Parguera, 20 m. Scale bar = 2.0 mm.

inconspicuous rhizoids. Chloroplasts are lens shaped, with many pyrenoids. Algae are shiny emerald green in color.

*Habitat and Comments*: Resembling a small *Valonia ventricosa* J. Agardh, the species in Puerto Rico is typically found in deeper water, usually growing on coralline algae or *Peyssonnelia* spp. It has been reported to 82 m depth in Puerto Rico (Ballantine et al. 2016). Puerto Rican specimens are nearly spherical, and specimens collected have been vesicles, measuring only to 7.0 mm diam. Page (1970) realized that *Halicystis osterhoutii* was the gametophyte in a biphasic life history, referring to the gametophytic generation as the “*Halicystis*-phase.” Sporophytes are not yet known in Puerto Rico. [Additional illustration: Kylin 1949: fig. 62; Taylor 1960: pl. 7: fig. 3.]

#### ***Derbesia vaucheriiformis* (Harv.) J. Agardh**

FIGURE 31

*Derbesia vaucheriiformis* (Harv.) J. Agardh 1887: 34.

*Basionym*: *Chlorodesmis vaucheriiformis* Harv. 1858: 30, pl. 40D.

*Puerto Rican Records*: As *Derbesia vaucheriaeformis*: Almodóvar and Blomquist 1965; Ballantine 1977; Almodóvar et al. 1979; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution*: North America, Bermuda, Bahamas, Cuba, Puerto Rico, Brazil, Venezuela.

*Other Distribution*: See Guiry and Guiry (2022)

*Type Locality*: Key West, Florida Keys, Monroe County, Florida, USA.

Filamentous sporophytes form dense tufts, 0.5–5.0 cm tall, of dichotomously branched siphons, 25–50 µm diam. Pedicellate sporangia, ovoid or broadly pyriform, replace branches. They measure 100–130 µm diam and 190–300 µm long. The pedicels are about 15 µm diam and 50–100 µm long. Gametophyte plants are not known from Puerto Rican collections.

*Habitat and Comments*: *Derbesia vaucheriiformis* occurs in protected areas near the low-tide line and into shallow waters. It is also sometimes entangled with or epiphytic on other larger algae. [Additional illustrations: Littler et al. 2008: 209.]

DICHOTOMOSIPHONACEAE G. M. SM.

Avrainvillea Decne.

Avrainvillea Decne. 1842a: 108.

Thalli are noncalcified, composed of a single conspicuous, unbranched stipe (lacking in a few species) that bears a single terete to compressed or bladelike flabellum or a branched stipe with a single terminal flabellum on each branch. Stipes arise above a spreading holdfast anchored by a sometimes spreading, subsediment or emergent mass of rhizoids often enmeshed with sand grains. Thalli are composed of structural dichotomously branched coenocytic filaments interwoven to form a loose or tight cortex. The filaments are cylindrical, torulose, or moniliform and constricted at or near the dichotomies. There are 30 recognized species of *Avrainvillea*, with 11 species and 3 infra-specific taxa occurring in Puerto Rico.

Notes: *Avrainvillea* and *Cladocephalus* were formerly placed within the Udoteaceae. Curtis et al. (2008) utilized molecular evidence to show that these two genera formed a clade with *Dichotomosiphon*. Subsequently, *Avrainvillea* and *Cladocephalus* have been recognized as belonging to the Dichotomosiphonaceae (Cremen et al. 2019; Guiry and Guiry 2022).

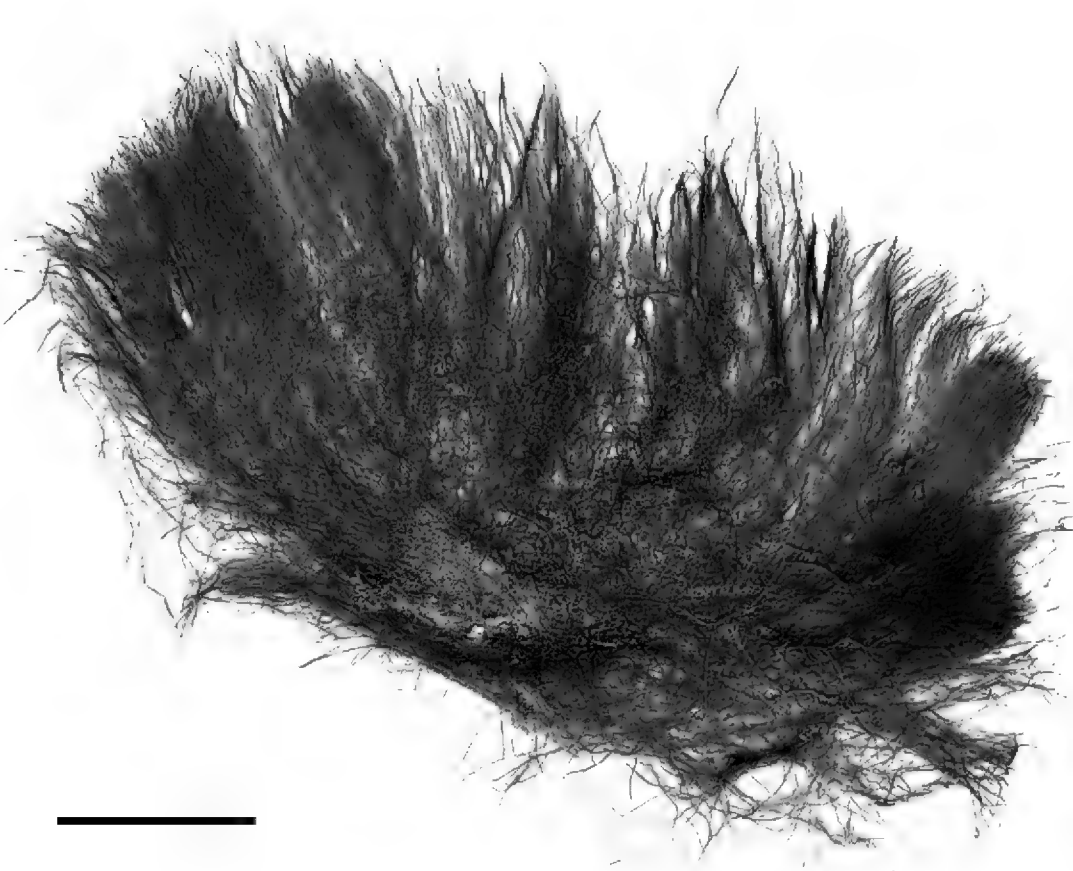


FIGURE 31. *Derbesia vaucheriiformis*. DLBsn, herbarium specimen: Algal plain, seaward Media Luna Reef, 17 m. Scale bar = 1.0 cm.

KEY TO THE AVRAINVILLEA SPECIES OF PUERTO RICO

- 1. Flabella digitate; medullary filaments with clavate apices ..... *A. digitata*  
Flabella flattened, peltate, or knob-like ..... 2
- 2. Flabella thickened or expanded and knob-like ..... *A. rawsonii*  
Flabella flattened ..... 3
- 3. Flabella supported by numerous stipes ..... *A. fenicalii*  
Flabella borne on single stipes ..... 4
- 4. Flabellum medullary filaments moniliform throughout ..... 5  
Flabellum medullary filaments not uniformly moniliform throughout ..... 7
- 5. Medullary filaments substantially distally narrowed ..... 6  
Medullary filaments not or only minimally distally narrowed ..... *A. nigricans*
- 6. Interior medullary filaments 60–140 µm in diameter; flabellum 2.0–5.0 mm thick ..... *A. fulva*  
Interior medullary filaments 45–80 µm in diameter; flabellum thinner, 1.0–2.0 mm thick .....  
..... *A. silvana*
- 7. Medullary filaments cylindrical throughout ..... *A. mazei*  
Medullary filaments partly moniliform and/or tortuous in shape ..... 8
- 8. Flabellum thickness > 4.0 mm ..... *A. longicaulis*  
Flabellum not as thick, <2.0 mm ..... 9
- 9. Flabellum base truncate, zonate; stipe short and thick; interior medullary filaments 30–45 µm in diameter .....  
..... *A. elliotii*  
Flabellum base cordate; interior medullary filaments < 25 µm in diameter ..... 10
- 10. Flabella large, to 24 cm tall, flabella zonate, deeply cordate; medullary filaments 12–20 µm in diameter .. *A. asarifolia*  
Flabella smaller, to 6.0 cm tall, flabella not zonate, shallowly cordate; medullary filaments 8.0–12 µm in diameter .....  
..... *A. levis*



***Avrainvillea asarifolia* Børgesen f. *asarifolia***

FIGURE 32A

*Avrainvillea asarifolia* f. *asarifolia* Børgesen 1909: 34, fig. 4, pl. 3.

**Puerto Rican Records:** Almodóvar and Ballantine 1983; Ballantine et al. 1987; Littler and Littler 1992; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

**Western Atlantic Distribution:** Belize, Panama, North America, Bahamas, Barbados, Cuba, Hispaniola, Jamaica, Martinique, Puerto Rico, St. Lucia, U.S. Virgin Islands, Colombia.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** St. Thomas, U.S. Virgin Islands.

Thalli are erect, 1.0–30 cm tall. Flabella measure 8.0–11 cm long, to 19 cm broad and less than 2.0 mm thick. The flabella are cuneate to cordate at the base and oblong reniform above. Flabella are terminal on terete stipes, 3.0–15(–20) cm long and 6.0–12 mm diam above a bulbous rhizoidal mass. Flabella normally possess zonate surfaces and mostly have entire and rounded margins. Internally, they are composed of smooth or slightly torulose medullary siphons, 20–40 µm diam (reported to be somewhat less in shallow-water forms), and cortical siphons more closely branched and moniliform, 12–20 µm diam. Stipes are composed of cylindrical filaments, 30–50 µm diam. Algae are a dull grayish green to dark green in color.

**Habitat and Comments:** *Avrainvillea asarifolia* occurs subtidally in sandy substrata down to 70 m depths in Puerto Rico. It is common on the Media Luna algal plain at 17 m depth offshore La Parguera. Taylor (1960) indicated it was apparently a deepwater species, dredged from 4.6 to 90 m depths. [Additional illustrations: Gepp and Gepp 1911: pl. 14, figs. 116–117; Littler and Littler 1992: fig. 1a–g; Cabrera et al. 2020: fig. 2.]

***Avrainvillea asarifolia* f. *olivacea* D. S. Littler et Littler**

FIGURE 32B

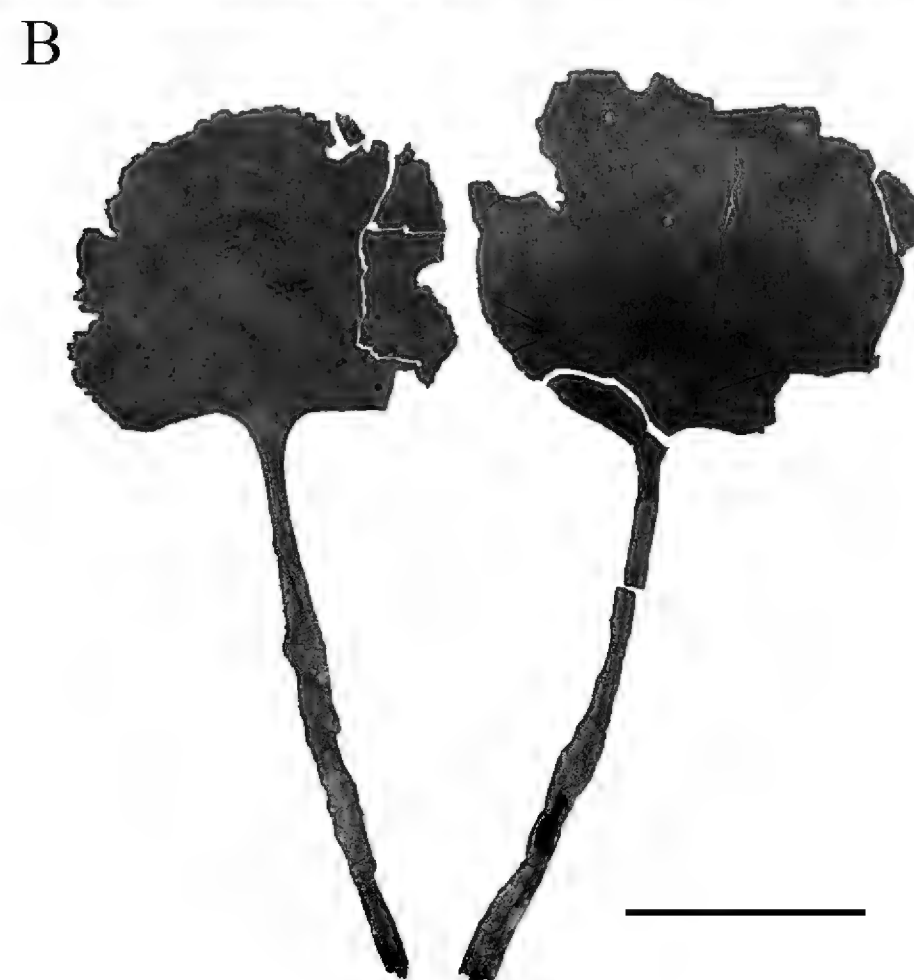
*Avrainvillea asarifolia* f. *olivacea* D. S. Littler et Littler 1992: 379, fig. 2a–e.

**Puerto Rican Record:** Littler and Littler 1992.

**Western Atlantic Distribution:** Belize, North America, Bahamas, Cuba, Jamaica, Puerto Rico, U.S. Virgin Islands.

**Type Locality:** Hidden Creek Lake, Twin Cays, Belizean Barrier Reef, Belize.

Although similar to *Avrainvillea asarifolia* f. *asarifolia*, *A. asarifolia* f. *olivacea* differs in its olive color and thinner flabella with a wider than long truncate lower margin that either lacks or has faint, indistinct zonation above an often extremely long, slender stipe. The form may have up to 12 clustered uprights from its stoloniferous rhizoidal base, compared to the solitary or 2–5 uprights of *A. asarifolia* f. *asarifolia*.



**FIGURE 32.** *Avrainvillea asarifolia*. (A) *A. asarifolia* f. *asarifolia*. In situ habit photograph from algal plain, seaward of Media Luna Reef, 17 m. Field = approximately 10 cm. (B) *A. asarifolia* f. *olivacea*. MDP7736, herbarium specimen: Joyuda. Scale bar = 5.0 cm.

**Habitat and Comments:** *Avrainvillea asarifolia* f. *olivacea* occurs in organically enriched mangrove creeks, lagoons, and saltwater ponds; the type specimen was collected in silt and peat substrata at 0.3–0.6 m depth. Littler and Littler (1992) assigned a specimen (fig. 31B), collected by Díaz-Piferrer (DLB7736) from Joyuda, SW Puerto Rico, as a paratype (US Alg. Coll. 094344).

***Avrainvillea digitata* D. S. Littler et Littler**

FIGURE 33

*Avrainvillea digitata* D. S. Littler et Littler 1992: 379, fig. 3a–f.*Puerto Rican Records:* Littler and Littler 1992; Ballantine and Aponte 1997a, 2002.*Western Atlantic Distribution:* Belize, Panama, Bahamas, Cayman Islands, Cuba, Grenadines, Jamaica, Puerto Rico.*Type Locality:* Low-water mark on rocks; Abraham Bay, Mari-guana (island), Bahamas.

Thalli are gregarious, with fingerlike or occasionally clavate or pointed uprights, up to 6.0 cm tall and 1.5 cm diam, above large prostrate masses up to 13 cm thick. Erect uprights lack a differentiated stipe, and the expanded bases are spongy in texture and composed of loosely interwoven siphons. Medullary and surface siphons

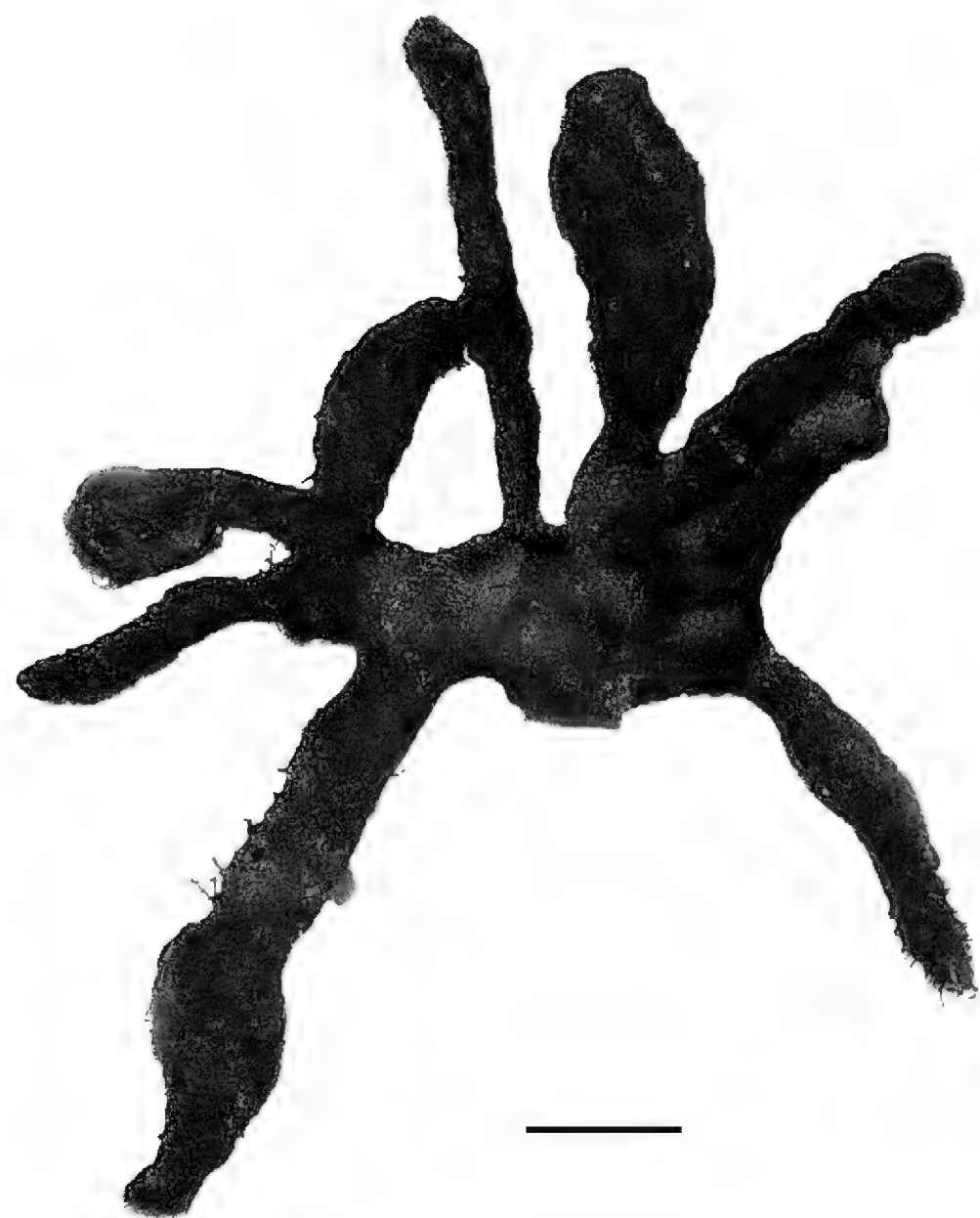


FIGURE 33. *Avrainvillea digitata*. DLB1413, herbarium specimen: Algal plain, seaward Media Luna Reef, 17 m. Scale bar = 2.0 cm.

are slightly moniliform, 40–55(–75)  $\mu\text{m}$  diam, and possess mostly bulbous apices. Algae are dark brownish green in color.

*Habitat and Comments:* *Avrainvillea digitata* typically occurs in *Thalassia testudinum* König seagrass beds and shallow-water habitats, less than 1.0 m deep. The shallow plants possess characteristic fingerlike uprights (Littler and Littler 1992: fig. 3a), whereas uprights of those from depths greater than 3.0 m are often narrower, with bluntly pointed tips. Puerto Rican specimens to 17 m depths possess more club-shaped uprights (Littler and Littler 1992, 2000). [Additional illustrations: Littler and Littler 1992: fig. 3a–f, 2000: 383.]

***Avrainvillea elliottii* A. Gepp et E. Gepp**

FIGURE 34

*Avrainvillea elliottii* A. Gepp et E. Gepp 1911: 35, 138, pl. 11: fig. 99, pl. 12: figs. 99a, 100.*Puerto Rican Records:* Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.*Western Atlantic Distribution:* North America, Cuba, Grenadines, Martinique, Puerto Rico, Brazil.*World Distribution:* See Guiry and Guiry (2022).*Type Locality:* Morne Rouge Bay, Grenadines, Lesser Antilles, West Indies.

Thalli are generally solitary or less frequently occur in clusters, reaching 6.0–13 cm tall above a small rhizoidal mass. The fan-shaped flabellum is truncate below and broadly expanded above, 3.5–8.0 cm long, 5.0–10 cm wide, and 4.0 mm or more thick. Flabellum medullary siphons are cylindrical to slightly moniliform and measure 20–34  $\mu\text{m}$  diam. Cortical siphons are slightly moniliform to tortuous, 18–30  $\mu\text{m}$  diam, some with hooked apices. Young flabellum margins are entire, becoming eroded or lobed and distinctly zonate. Stipes are cylindrical to slightly compressed, 1.0–4.0 cm tall and 0.6–1.0 cm diam, and composed of cylindrical to slightly moniliform medullary siphons, 30–44  $\mu\text{m}$  diam, and cortical siphons, tortuous to slightly moniliform, 20–28  $\mu\text{m}$  diam. Algae are brownish in color.

*Habitat and Comments:* Although uncommon in Puerto Rico, *Avrainvillea elliottii* usually occurs on sandy bottoms in shallow water at 2.0–10 m depths; it has also been collected at Punta Caracoles, Arecibo, in deeper water, 55 m depths (Ballantine et al., 2016). [Additional illustrations: Littler and Littler 1992: fig. 4a–f, 2000: 385.]



FIGURE 34. *Avrainvillea elliottii*. DLB659, herbarium specimen: Edge of insular shelf, offshore from Guánica, 19 m. Scale bar = 2.0 cm.

***Avrainvillea fenicalii* D. S. Littler, Littler,  
et M. Hay f. *flabellifolia* D. S. Littler, Littler, et M. Hay**

FIGURE 35

*Avrainvillea fenicalii* D. S. Littler, Littler, et M. Hay f. *flabellifolia* D. S. Littler, Littler, et M. Hay in D. S. Littler and Littler 1992: 384, fig. 6a–e.

*Puerto Rican Records:* Littler and Littler 1992; Ballantine and Aponte 2002.

*Western Atlantic Distribution:* Puerto Rico, U.S. Virgin Islands.

*Type Locality:* Between Jack's Bay and Isaac Bay, St. Croix, U.S. Virgin Islands.



FIGURE 35. *Avrainvillea fenicalii* f. *flabellifolia*. AJB62-33, herbarium specimen: Cayo Santana, La Parguera. Scale bar = 5.0 cm.



Thalli are up to 7.0 cm tall, forming clusters of up to 8 uprights, each stipe, to 1.0 cm diam, arising from a massive sub-sediment rhizoidal mass and bearing fanlike flabella. Individual flabella are entire to broadly lobed and distinctly zonate. The flabella measure 26–45(–75) mm long and 30–60 mm wide. Stipe siphons are somewhat moniliform, cylindrical, or tortuous. Medullary stipe siphons measure 40–52  $\mu\text{m}$  diam, and the cortical siphons are 8–20  $\mu\text{m}$  diam. Flabellum medullary siphons vary from slightly moniliform to cylindrical to tortuous. The flabellum medullary siphons are 20–30  $\mu\text{m}$  diam, and the slightly moniliform cortical flabellum siphons are 16–29  $\mu\text{m}$  diam, tapering to 8.0  $\mu\text{m}$  diam, and are rounded, clavate, hooked, or distorted at their apices.

**Habitat and Comments:** Although the two known forms of *Avrainvillea fenicalii* are similar in siphon shape and size, with large, basal pigmented columnar masses, they differ primarily in blade shape. *Avrainvillea fenicalii* f. *flabellifolia* has an entire or broadly lobed flabellum in one plane, with distinct zonation, whereas *A. fenicalii* f. *fenicalii* has a palmate flabellum of numerous, deeply lacerated, paddle-shaped to highly irregular blades in more than one plane that lack zonation (cf. Littler and Littler 1992: fig. 5a,b).

Although apparently uncommon in Puerto Rico, *Avrainvillea fenicalii* f. *flabellifolia* occurs in shallow water in sandy soft sediments and coarse sands associated with *Thalassia*. Collected by A. J. Bernatowicz in 1962 (US Alg. Coll. 37998), it was reported as being abundant among *Thalassia* at Cayo Santana, La Parguera (Littler and Littler 1992: 387).

### ***Avrainvillea fulva* (M. Howe) D. S. Littler et Littler**

FIGURE 36

*Avrainvillea fulva* (M. Howe) D. S. Littler et Littler 1992: 387, fig. 7a–e.

**Basionym:** *Avrainvillea nigricans* f. *fulva* M. Howe in Collins et al. 1908: P.B.A. no. 1480.

**Puerto Rican Records:** As *Avrainvillea fulva*: Littler and Littler 1992; Ballantine and Aponte 1997a, 2002.

**Western Atlantic Distribution:** North America, Bermuda, Bahamas, Barbados, Cayman Islands, Cuba, Guadeloupe, Jamaica, Martinique, Puerto Rico, Colombia, Venezuela.

**Type Locality:** Castle Island (off SW end of Acklins Island), Bahamas.

Thalli are up to 24 cm tall, occurring in clusters of 2–5 uprights or rarely solitary. Each stipe bears a single wedge-shaped flabellum, lacking zonation and measuring to 18 cm long, 15 cm wide, and 2.0–5.0 mm thick. Thalli are anchored below by a massive, subsediment rhizoidal system. Flabella are initially smooth and curved, becoming fibrous and lacerated and eroded with age. Flabellum medullary siphons are moniliform or occasionally cylindrical, 60–120(–140)  $\mu\text{m}$  diam. Flabellum cortical siphons are moniliform, repeatedly branched, and tapering to



FIGURE 36. *Avrainvillea fulva*. MDP4927, herbarium specimen: Havana, Cuba, 1.0 m. Scale bar = 1.0 cm.

20–40  $\mu\text{m}$  diam in the final 2–3 dichotomies. Siphons, 42–55  $\mu\text{m}$  diam, along the growing margin possess few dichotomies and do not taper. Unbranched stipes are cylindrical, measuring up to 6.0 cm long and thick, up to 4.5 cm diam. The stipes gradually taper upward from base, often becoming compressed near flabellum. Stipe medullary siphons are moniliform and 80–130  $\mu\text{m}$  diam, and stipe cortical siphons are moniliform or tortuous and 20–40  $\mu\text{m}$  diam. Rhizoids measure up to 85  $\mu\text{m}$  diam. Algae are green to golden green in color.

**Habitat and Comments:** *Avrainvillea fulva* occurs in lagoons and moderately shallow-water habitats in 1.0–10 m depths, in soft, organic rich substrata and sand-covered rocks. [Additional illustrations: as *Avrainvillea nigricans*, Howe 1907: 504, pl. 28: figs. 8–25; Vickers 1908: pl. 30: figs. 1–6.]

### ***Avrainvillea levis* M. Howe**

FIGURE 37

*Avrainvillea levis* M. Howe 1905: 565, pl. 23: fig. 1, pl. 26: figs. 8–10.

**Synonyms:** *Avrainvillea sordida* (Montagne) P. Crouan et H. Crouan in Mazé and Schramm 1878: 89 [non *Udotea sordida* Montagne 1844: 659, which is now *Avrainvillea erecta* (Berkeley) A. Gepp et E. S. Gepp 1911: 29]; *Avrainvillea sordida* (Crouan) Murray et Boodle 1889: 70, nom. illeg.

**Puerto Rican Records:** Almodóvar and Blomquist 1965; Almodóvar and Ballantine 1983; Littler and Littler 1992; Ballantine and Aponte 2002.

**Western Atlantic Distribution:** North America, Bahamas, Cayman Islands, Cuba, Hispaniola, Jamaica, Martinique, Puerto Rico, St. Lucia, Turks and Caicos.

**Type Locality:** Cave Cay, Exuma Chain, Bahamas.

Thalli are up to 11 cm tall, with simple (or occasionally branched) stipes that arise from conical rhizoidal bases. Each stipe bears a thin, less than 1.0 mm thick, tough flabellum, that is broadly rounded to reniform. Flabella measure 4.0–7.0 cm long and 5.0–9.0 cm wide. Flabella, typically with a distinctive cordate base, are somewhat spongy and thin, with faint to no zonation. Flabellum medullary siphons are smooth to slightly moniliform and constricted above dichotomously branched forks, 20–35(–40)  $\mu\text{m}$  diam. Flabellum cortical siphons are cylindrical to slightly moniliform, 12–20  $\mu\text{m}$  diam, decreasing to 6.0–12  $\mu\text{m}$  diam at the surface. Stipes are cylindrical or slightly flattened, 0.5–2.5(–5.0) cm long and 4.0–6.0 mm diam. Stipe medullary siphons are cylindrical to slightly moniliform, 25–40  $\mu\text{m}$  diam. Stipe cortical siphons are slightly moniliform and tapering to 8.0–12(–20)  $\mu\text{m}$  diam with rounded apices. Algae are dull yellow green to gray-brownish green in color.

**Habitat and Comments:** The type was collected under a rock overhang near the low-water mark (Howe 1905). In Puerto Rico *Avrainvillea levis* is more common in shallow waters up to 1.0 m

deep; however, the species also occurs on sand plains to depths of 90 m. Howe (1905: 566) noted that his *Avrainvillea levis* was taxonomically the same as “*A. sordida* (Mont.) P. Crouan et H. Crouan (in Mazé and Schramm 1877).” It was earlier cited without reference to the basionym, *Udotea sordida* Mont. (1844), as “*A. sordida* Crn.” by Murray and Boodle (1889: 70) but with a description based on Crouan specimens from Guadeloupe (Nos. 80, 174[bis] in Mazé and Schramm 1878) and a Murray collection from Grenadines. Taxonomically, *Udotea sordida* Montagne is now a synonym of *Avrainvillea erecta* (Berk.) A. Gepp et E. S. Gepp (1911: 29). [Additional illustrations: Littler and Littler 1992: fig. 10a–e, 2000: 387.]



FIGURE 37. *Avrainvillea levis*. DSL17048b, herbarium specimen: West side Monito Island, 40 m. Scale bar = 2.0 cm.



***Avrainvillea longicaulis* (Kütz.) G. Murray et Boodle f. *longicaulis***

FIGURE 38A

*Avrainvillea longicaulis* (Kütz.) G. Murray et Boodle 1889: 70, pl. 288: figs. 1–5.

*Basionym*: *Rhipilia longicaulis* Kütz. 1858: 13, pl. 28: fig. IIc,d.

*Puerto Rican Records*: As *Avrainvillea longicaulis*: Almodóvar and Blomquist 1959; Almodóvar 1964a, 1971; Almodóvar and Pagán 1971; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution*: Belize, Mexico, Panama, North America, Bermuda, Bahamas, Barbados, Antigua, Cayman Islands, Cuba, Grenadines, Jamaica, Martinique, Puerto Rico, U.S. Virgin Islands, Brazil, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: “Ad Antilles” (Kützing 1858: 13); Antigua (Littler and Littler 1992: 394: locale on the basis of type specimen: Sonder Herbarium, MEL).

Thalli are 13–22 cm tall with stipes single or in clusters of 2–5, arising from a large rhizoidal base. Flabella are thick and spongy, with or without faint zonation, and measure 6.0 cm long and 10.5 cm broad. They are rounded, obovate, or spatulate, most with smooth, rounded margins and a cuneate-rounded base. Flabellum medullary siphons are mostly cylindrical or occasionally moniliform, 28–70  $\mu\text{m}$  diam, with each siphon branch constricted at the base. Flabellum cortical siphons are moniliform and tapering to 15–25  $\mu\text{m}$  diam. The stipes are cylindrical, compressed or flattened, measuring 3.0–12 cm long and 5.0–13 mm diam. Stipe medullary siphons are cylindrical and 38–46  $\mu\text{m}$  diam. Stipe cortical siphons are moniliform or irregular, 8–12  $\mu\text{m}$  diam.

*Habitat and Comments*: In Puerto Rico, *Avrainvillea longicaulis* occurs in protected habitats in shallow water, 1.0–4.0 m deep, in sand and mud substrata. Taylor (1960: 160) also reported the species to “to a depth of 30 m.” [Additional illustrations: Murray 1889: pl. 288, figs. 1–5; Vickers 1908: pl. 31; Taylor 1960: pl. 19: fig. 1; Littler and Littler 1992: fig. 12a–e, 2000: 389, 411; Santos and Nunes 2015: fig. 3a–i.]

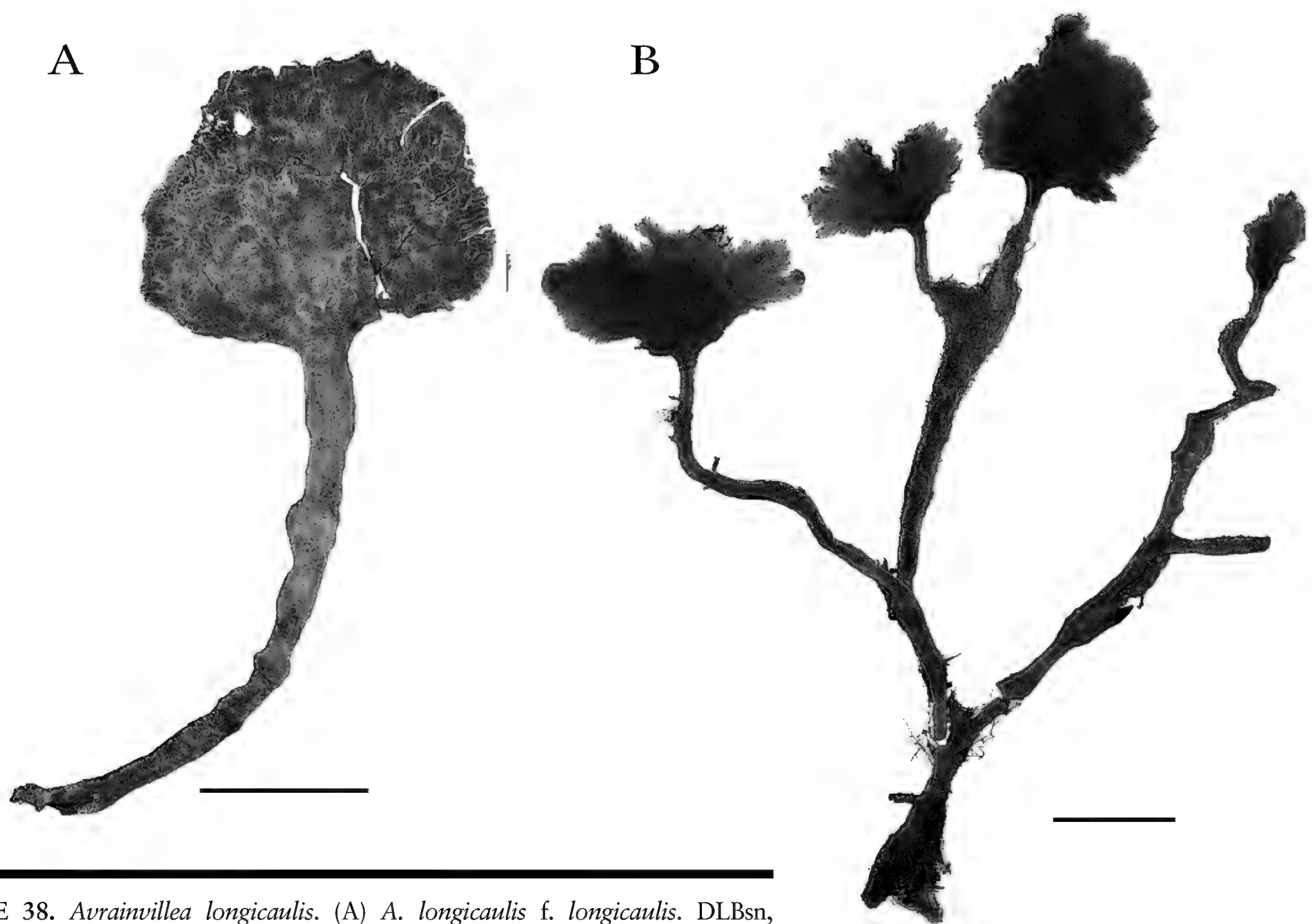


FIGURE 38. *Avrainvillea longicaulis*. (A) *A. longicaulis* f. *longicaulis*. DLBsn, herbarium specimen: Bahia Montalva. Scale bar = 5.0 cm. (B) *A. longicaulis* f. *laxa*. JN14999, herbarium specimen: Leeward Guayacan Island, La Parguera. Scale bar = 5.0 cm.

***Avrainvillea longicaulis* f. *laxa* D. S. Littler et Littler**

FIGURE 38B

*Avrainvillea longicaulis* f. *laxa* D. S. Littler et Littler 1992: 397, fig. 13a–e.

**Puerto Rican Records:** Littler and Littler 1992. As *Avrainvillea longicaulis*: Almodóvar and Ballantine 1983.

**Western Atlantic Distribution:** Belize, North America, Bermuda, Cuba, Puerto Rico.

**Type Locality:** Tobacco Range, Belize Barrier Reef, Belize.

Thalli are to 30 cm tall, with an exceptionally long cylindrical to flattened stipe, up to 26 cm in length and 1.0 cm in diameter. Stipes are frequently branched, with each single stipe bearing a thin elongate to oval flabellum with a curving cuneate lower portion. The flabella measure to 19 cm long and to 7.0 cm wide. Flabella are thin, <3.0 mm thick, composed of medullary siphons, 40–60  $\mu\text{m}$  diam in mature blades, and taper to 8.0–12(–25)  $\mu\text{m}$  diam in the lower third of flabella. Cortical siphons of the growth margin are cylindrical, thick walled, and 20–30  $\mu\text{m}$  diam. Stipe medullary siphons are moniliform and (20–)38–60  $\mu\text{m}$  diam, and cortical stipe siphons are 8.0–12  $\mu\text{m}$  diam.

**Habitat and Comments:** *Avrainvillea longicaulis* f. *laxa* grows in nutrient-rich, soft, fine organic sediment on bottoms of shallow interior lagoons and channels of mangrove islands. The taxon is conspicuous in the broad mangrove channels, 1.0–2.0 m deep, behind Isla Guayacan, off La Parguera. *Avrainvillea longicaulis* f. *laxa* differs from *A. longicaulis* f. *longicaulis* in being taller with more elongate flabella. Furthermore, *A. longicaulis* f. *laxa* grows in mangrove channels and lagoons, and *A. longicaulis* f. *longicaulis* is encountered in seagrass beds. [Additional illustrations: Littler and Littler 1992: fig. 13a–e, 2000: 389.]

***Avrainvillea mazei* G. Murray et Boodle**

FIGURE 39

*Avrainvillea mazei* G. Murray et Boodle 1889: 70.

**Heterotypic Synonym:** *Flabellaria fimbriata*? sensu Mazé and Schramm 1878: 89; non *Flabellaria fimbriata* Chauv. 1842: 123 [= *Codium flabelliforme* (Desf.) C. Agardh 1823: 455, which is now *Udotea flabelliformis* (Desf.) P. Crouan et H. Crouan in Schramm and Mazé 1866: 104].

**Western Atlantic Distribution:** Mexico, North America, Bermuda, Cuba, Guadeloupe, Puerto Rico.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Grand Bourg, Île de Marie Galante, Guadeloupe, French West Indies; based on lectotype chosen by Littler and Littler (1992). Murray and Boodle (1889: 71) cited specimens from two localities listed by Mazé and Schramm (1878: 89–90): “Ad ins. Guadeloupe” (as “*Flabellaria fimbriata*? Chauv. 1842: 123” [Mazé No. 65 1st Série]) and “ad ins. Marie Galante prope la Guadeloupe” (as “*Avrainvillea sordida*



FIGURE 39. *Avrainvillea mazei*. LRA4648, herbarium specimen: Aguirre, Cayo Caribe, Jobos. Scale bar = 1.0 cm.

var. *longipes* P. Crouan et H. Crouan” [Mazé and Schramm No. 1234]). Littler and Littler (1992: 397) selected the Mazé No. 65 1st Série (PC) specimen as a lectotype.

Representing a new Puerto Rican record, this US Alg. Coll. specimen was annotated to be *Avrainvillea mazei* by D. S. Littler: SE tip of Cayo Caribe, Jobos, Aguirre, Puerto Rico (US Alg. Coll. 51620, LRA4648, as “*A. rawsonii*,” 11.X.1962). Thalli reach up to 15 cm tall and are solitary or occur in closely grouped clusters, above a massive rhizoidal base. Mature flabella are cuneate to wedge shaped, coarse, and not zonate with smooth to ragged growth margins. Flabella measure up to 7.0 cm long, 9.0 cm wide, and more than 2.0 mm thick. Flabellum medullary siphons are cylindrical, rarely moniliform, (40–)50–60(–80)  $\mu\text{m}$  diam, and cortical siphons are smaller in the growing margin, 30–40  $\mu\text{m}$  diam. Stipes are cylindrical to slightly compressed, up to 8.0 cm long and 1.2 cm diam. Stipe medullary siphons are unbranched and possess thick walls; they are cylindrical or rarely slightly compressed or tortuous, 55–70  $\mu\text{m}$  diam. Cortical stipe siphons are moniliform, 12–18  $\mu\text{m}$  diam. Algae are bright green in color.

**Habitat and Comments:** *Avrainvillea mazei* occurs in sandy or seagrass habitats in shallow water. [Additional illustrations: Gepp and Gepp 1911: 9, pls. 82–83, pl. 10: fig. 81; Littler and Littler 1992: fig. 14a–f, 2000: 389.]

***Avrainvillea nigricans* Decne.**

FIGURE 40

*Avrainvillea nigricans* Decne. 1842a: 108.

*Puerto Rican Records:* Almodóvar and Blomquist 1961; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Belize, Mexico, North America, Bahamas, Antigua, Barbados, Cuba, Guadeloupe, Honduras, Martinique, Netherlands Antilles, Puerto Rico, St. Lucia, Turks and Caicos, U.S. Virgin Islands, Brazil.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Îles de Saintes, Guadeloupe, French West Indies.

Thalli are up to 30 cm tall, usually solitary or less frequently with 2–5 uprights, each bearing a flabellum on a stipe that arises from a bulbous rhizoidal base. Flabella are terete below and transition into a flattened to suborbicular, irregularly lobed blade up to 15 cm long and 23 cm broad. Flabella are thin, less than 2.0 mm thick, with smoothly rounded, lacerate, or ragged margins. Flabellum medullary and cortical siphons are both strongly moniliform and 30–40  $\mu\text{m}$  diam. Stipes are cylindrical and unbranched, up to 9.0 cm long and 3.0–7.0 mm diam, rarely branched. Stipe medullary siphons are slightly moniliform and 30–60  $\mu\text{m}$  diam. Stipe cortical siphons are strongly moniliform and 10–20  $\mu\text{m}$  diam. Algae are pale to dark greenish brown or blackish.

*Habitat and Comments:* *Avrainvillea nigricans* occurs mostly in sheltered, shallow waters near mangroves, in seagrass beds, and in sand flats, and subtidally down to depths of 30–45 m. *Avrainvillea nigricans* is a common, highly variable species with many recognized forms (see Littler and Littler 1992). Some Caribbean records of *A. nigricans* should be reexamined and compared against *A. fulva*. [Additional illustrations: Gepp and Gepp 1911: pl. 9, figs. 78–81; Taylor 1960: pl. 19: fig. 2, pl. 25: figs. 11, 12; Littler and Littler 1992: fig. 15a–f; Huisman 2015: fig. 25A–C; Santos and Nunes 2015: fig. 3a–g.]

***Avrainvillea rawsonii* (Dickie) M. Howe**

FIGURE 41

*Avrainvillea rawsonii* (Dickie) M. Howe 1907: 510, pl. 30.

*Basionym:* *Rhipilia rawsonii* Dickie 1874a: 151, pl. 11: figs. 1, 2.

*Puerto Rican Records:* As *Avrainvillea rawsonii*: Howe 1915; Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar 1962, 1964a; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Littler and Littler 1992; Ballantine and Aponte 1997a, 2002.

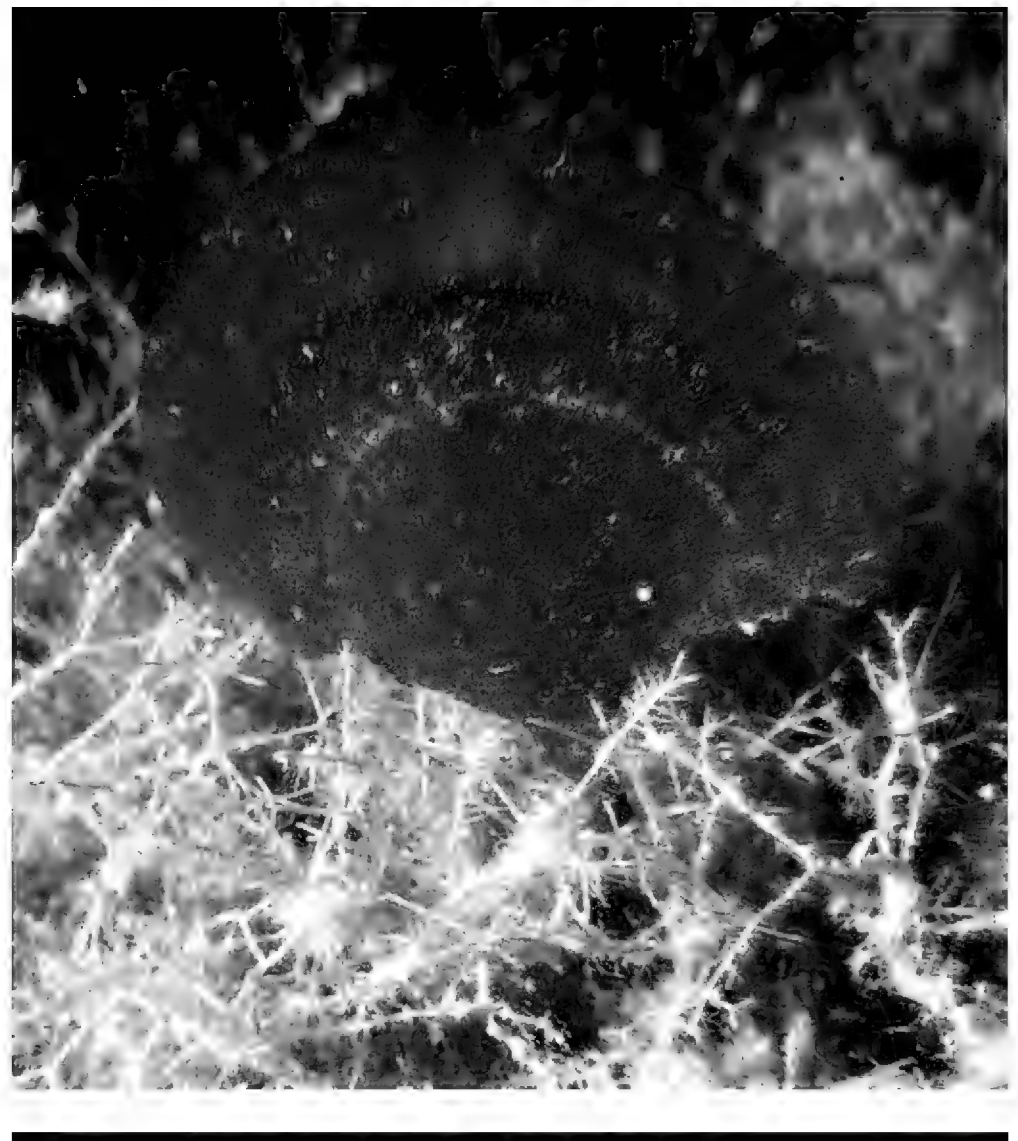


FIGURE 40. *Avrainvillea nigricans*. In situ habit photograph from algal plain, seaward Media Luna Reef, 17 m. Field = approximately 10 cm.

*Western Atlantic Distribution:* Costa Rica, Mexico, Panama, North America, Bermuda, Bahamas, Antigua, Barbados, Cayman Islands, Cuba, Hispaniola, Martinique, Netherlands Antilles, Nicaragua, Puerto Rico, St. Kitts, Trinidad and Tobago, Turks and Caicos, Colombia, Venezuela.

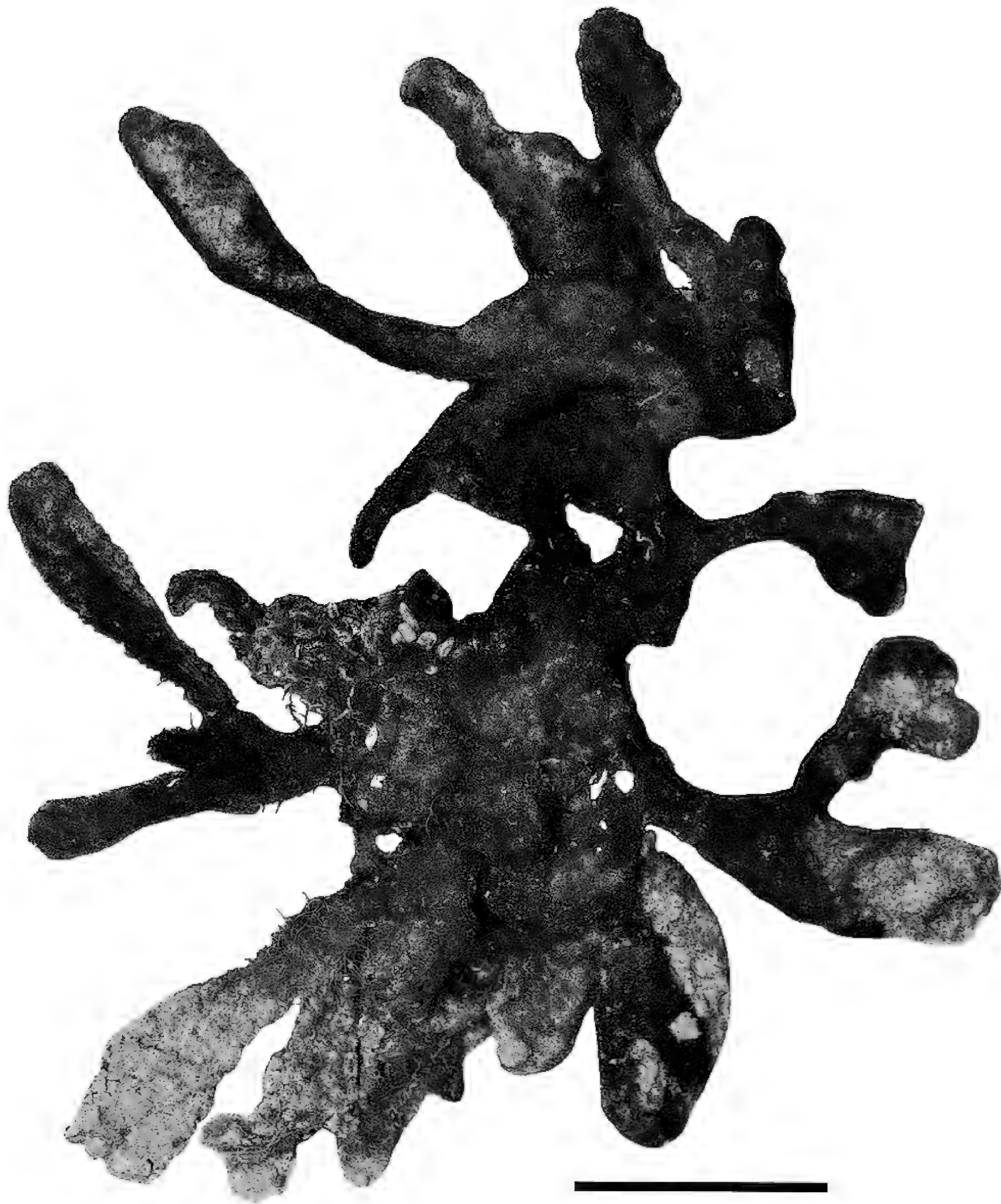
*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Barbados.

Thalli 4.0–12 cm tall, 0.5–5.0 cm wide, and 3.0 cm thick with uprights of variable shapes, ranging from nonbladeliike, spathulate forms with rounded or lobed growing margins. Algae are nonzonate and spongy. Uprights grow more or less gregariously, arising from large, prostrate rhizoidal mats, 20–30 cm in extent. Medullary and cortical siphons of upright portions are moniliform (cylindrical or submoniliform in dried specimens), 50–68(–80)  $\mu\text{m}$  diam. In shallow water, uprights lack distinctive stalks and are knob-like or irregularly clavate. In deeper water, uprights are thickly spathulate with a cylindrical to oval stalk-like portion. Algae are dull green to brownish green or blackish green in color.

*Habitat and Comments:* *Avrainvillea rawsonii* occurs on rocks and in sandy habitats in shallow water (usually less than 1.0 m depth) and deeper water, 10–25 m. [Additional illustrations: Gepp and Gepp 1911: pl. 8: fig. 76, pl. 9: fig. 77; Littler and Littler 1992: fig. 19a–f.]





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FIGURE 41. *Avrainvillea rawsonii*. DLB2959, herbarium specimen: Sandy Point, St. Croix, U.S. Virgin Islands. Scale bar = 2.0 cm.

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***Avrainvillea silvana* D. S. Littler et Littler**

FIGURE 42

*Avrainvillea silvana* D. S. Littler et Littler 1992: 408, fig. 20a–g.

*Puerto Rican Records:* Littler and Littler 1992; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Belize, Bahamas, British Virgin Islands, Cuba, Jamaica, Martinique, Puerto Rico, St. Barthélemy, U.S. Virgin Islands, Brazil.

*Type Locality:* Tobacco Range, NW fracture area, Belize Barrier Reef, Belize.

Thalli are up to 17 cm tall, with mostly solitary or rarely clustered stipes above a small fibrous rhizoidal mass. Flabella are terminal on simple or seldom branched terete stipes, up to 7.0 cm in length and to 7.0 mm diam. The ovate flabella, 11 cm long, 16 cm wide, and 1.0–2.0 mm thick, are smooth and mostly not zonate or with faint zonation. Flabella possess lacerate to ragged apical margins, and lower margins are attenuate or cuneate in shallow-water plants and flat or truncate in deepwater specimens. Flabellum medullary siphons are moniliform to cylindrical and thin walled, 45–80  $\mu\text{m}$  diam. Flabellum cortical siphons are tightly arranged; they are moniliform, with wide-spreading dichotomies that taper abruptly to 20  $\mu\text{m}$  diam, and possess rounded, hooked, or tortuous apices. The stipe medullary siphons are moniliform to occasionally cylindrical, measuring 45–80  $\mu\text{m}$  diam, and the stipe cortex is of tightly intertwined

siphons, moniliform and/or tortuous, often hyaline, 15–20  $\mu\text{m}$  diam. Algae are olive green in color.

*Habitat and Comments:* *Avrainvillea silvana* occurs in the shallow intertidal and mangrove habitats (1.0 m depth) and offshore sand plains and deepwater habitats, 25–117 m depths. [Additional illustrations: Littler and Littler 1992: fig. 20a–g, 2000: 393.]

***Cladocephalus* M. Howe**

*Cladocephalus* M. Howe 1905.

Thalli are erect and uncalcified, up to 14(–30) cm tall. The flattened flabella are single or multiple above distinct stipes, 2.0–7.0 mm long, arising from a base of matted rhizoids. Flabella are variously shaped and composed of pigmented medullary siphons parallel to each other. The medullary siphons are smooth and sparingly dichotomously branched, and the flabellum cortex is distinct from the medulla, being composed of inner cortical siphons that are repeatedly, dichotomously branched with wide-angled forks and outer more slender, branched, nonpigmented cortical siphons that form a dense outer cortex.

Although superficially similar to some *Avrainvillea* species, the two genera differ in their internal anatomy. The flabella and stipes of *Cladocephalus* have a medulla of pigmented green siphons and a cortex of interwoven transparent siphons, whereas cortical siphons are pigmented in *Avrainvillea*. Three species of *Cladocephalus* are currently recognized, one of which occurs in Puerto Rico.

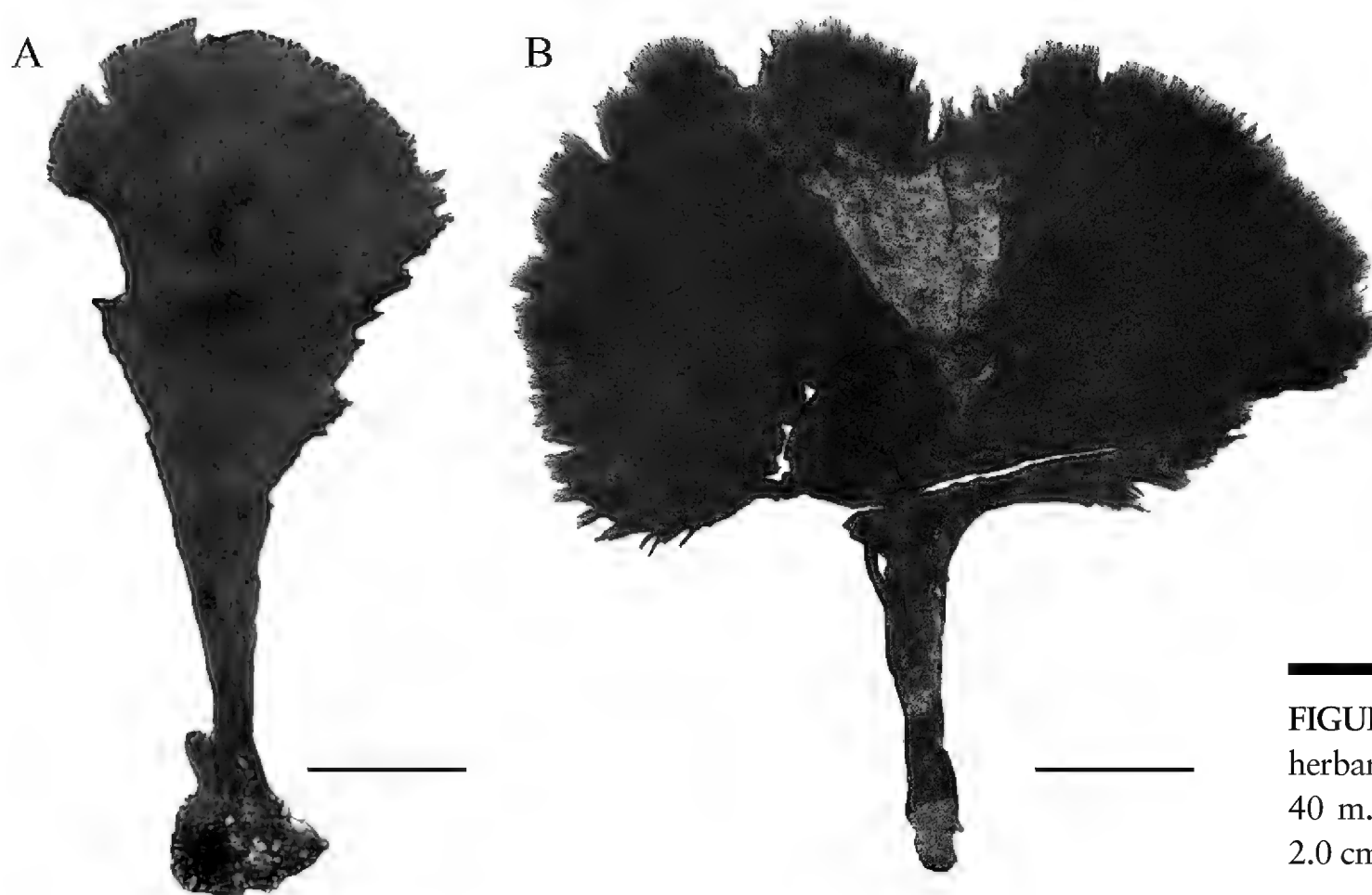


FIGURE 42. *Avrainvillea silvana*. D&ML17021, herbarium specimens: West side Monito Island, 40 m. (A) Scale bar = 1.0 cm; (B) scale bar = 2.0 cm.



***Cladocephalus luteofuscus* (P. Crouan et H. Crouan) Børgesen**

FIGURE 43

*Cladocephalus luteofuscus* (P. Crouan et H. Crouan) Børgesen 1909: 44.

*Basionym:* *Flabellaria luteofusca* P. Crouan et H. Crouan in Mazé and Schramm 1878: 88.

*Synonym:* *Udotea luteofusca* (P. Crouan et H. Crouan) M. Howe 1907: 513.

*Puerto Rican Records:* As *Cladocephalus luteofuscus*: Almodóvar and Blomquist 1965; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution:* Mexico, North America, Bermuda, Cuba, Martinique, Puerto Rico, St. Martin, U.S. Virgin Islands, Venezuela.

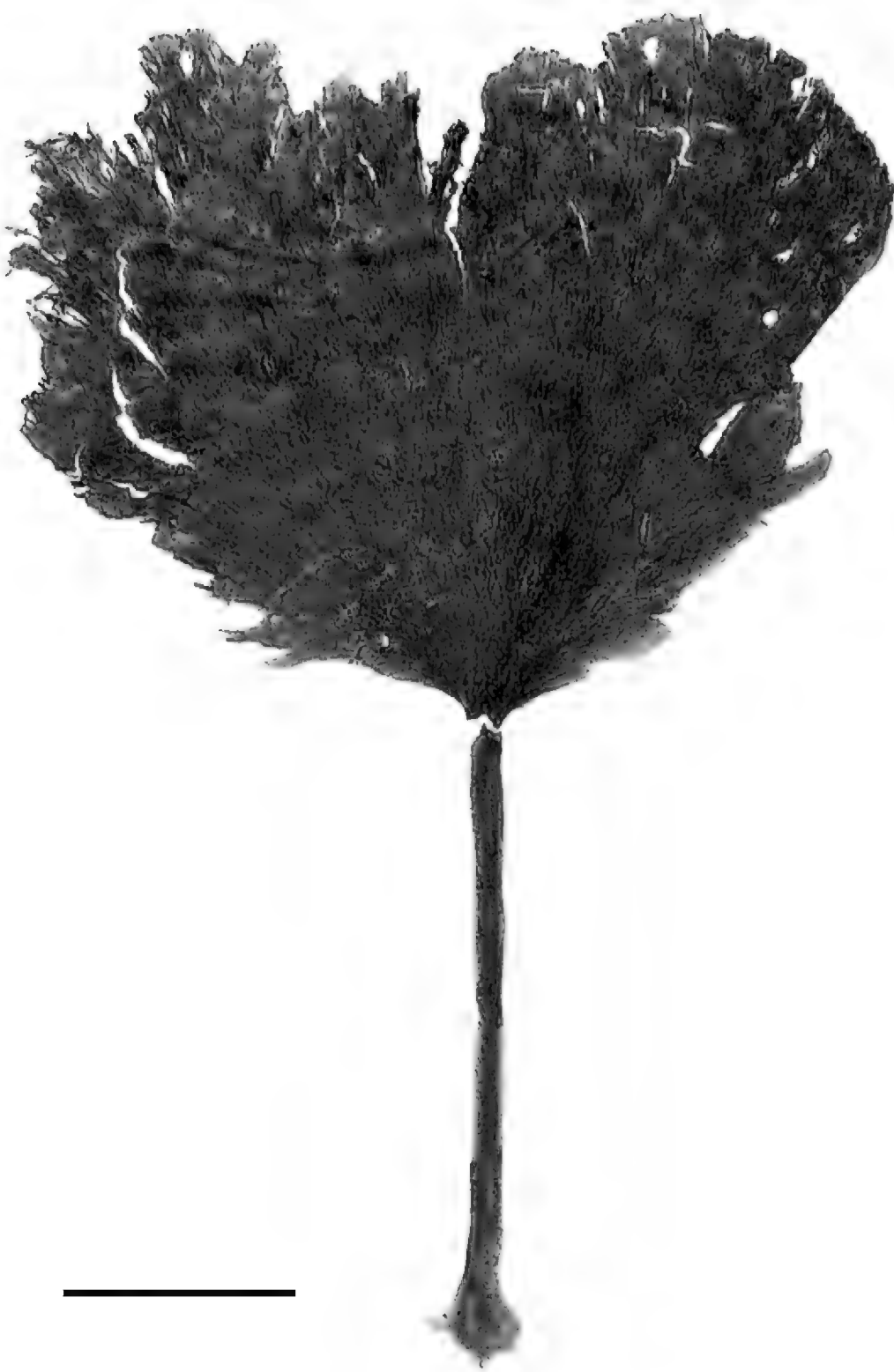


FIGURE 43. *Cladocephalus luteofuscus*. DLB4127, herbarium specimen: Punta Caracoles, Arecibo, 55 m. Scale bar = 1.0 cm.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Lac Simpson, near the pier of Durat, Anse du Marigot, Saint-Martin (Mazé and Schramm 1878: 88), Leeward Islands, Lesser Antilles, West Indies.

Thalli reach up to 20 cm tall and possess a thin, flattened, faintly zonate flabellum. The flabellum is transversely oval to wedge-like with a cuneate rounded or truncate base. The flabella measure 4.0–5.5 cm long and up to 8.0 cm wide above a stipe that arises from a bulbous rhizoidal mass. Flabella are composed of somewhat parallel, pigmented medullary siphons. These siphons, 30–80 µm diam, are cylindrical or slightly tortuous and decrease in diameter outward to a distinct cortex of densely interwoven, colorless cortical filaments, 4.0–10 µm diam. Flabellum siphons are branched repeatedly, dichotomously or sometimes irregularly. The stipes are often branched, either flattened below the flabellum or channeled, 2.0–10 cm long and 2.0–6.0 mm diam. The stipe siphons are composed of a cortex of interwoven transparent siphons and medulla of green pigmented siphons. Algae are dark yellow green in color.

*Habitat and Comments:* *Cladocephalus luteofuscus* is generally found in shallow seagrass beds and mangrove lagoons and channels to 5.0 m depths. The type was collected in muddy sand substratum. The species has only rarely been collected in Puerto Rico, where it occurs to depths of 55 m (Ballantine et al. 2016). *Cladocephalus luteofuscus* is elsewhere reported as having been dredged in deep water from 14 to 72 m (Taylor 1960), and from very shallow water, less than 1.0 m depth, in Bermuda (Schneider et al. 2010). [Additional illustrations: Gepp and Gepp 1911: pl. 4: figs. 32–35; Børgesen 1913: figs. 77, 78; Littler et al. 2008: 227.]

**HALIMEDACEAE LINK**

**HALIMEDEAE LINK**

***Halimeda* J. V. Lamour.**

*Halimeda* J. V. Lamour. 1812, nom. et typ. cons.

Thalli are coenocytic, arising from rhizoidal holdfasts. Algae are branched and composed of calcified segments that are separated briefly by noncalcified fused or nonfused filaments that connect the segments. The noncalcified nodes are flexible joints. Calcified segments are often flattened and vary in shape, appearing moniliform, discoid, spherical, or irregular. Segment medullary siphons are longitudinally arranged and branched. They bear expanded utricles that give rise to further series of utricles that terminate in an outer cortex. Terminal utricles are laterally adherent, forming a continuous cortex. Fourteen *Halimeda* species and one infraspecific taxon are known to Puerto Rico of a total of 47 species recognized worldwide.

KEY TO THE *HALIMEDA* SPECIES OF PUERTO RICO

1. Thalli of short stature, <2.6 cm tall ..... 2  
Thalli substantially taller ..... 3
2. Branching irregular; segments irregularly shaped ..... *H. hummii*  
Branching dichotomous; segments slightly wider than long ..... *H. pumila*
3. Thalli originating in more than one plane, forming large cushion-like mounds, basally anchored to the substratum by multiple rhizoidal attachments ..... *H. opuntia*  
Thalli originating in one plane, single basal attachment normally evident ..... 4
4. Uppermost segments terete ..... *H. monile*  
Segments flat or mostly flat ..... 5
5. Segment margins essentially entire ..... 6  
Segment margins lobed, irregular, or crenate ..... 8
6. Plants to 70 m long, frequently pendant over steep reef overhangs, segment surface slightly glossy ... *H. copiosa* (in part)  
Plants not as above ..... 7
7. Basally with 1 or more stalk-like segments; upper segments to 1.5 cm broad ..... *H. tuna*  
Basally without a stalk or at most a single little-differentiated cell; upper segments to 2.0–4.0 cm broad .. *H. discoidea*
8. Segments connected by a single siphon at joints; almost exclusively found in water deeper than 60 m ..... 9  
Segments joined by 2 or more siphons; species from shallow and/or deep water ..... 10
9. Upper margins of segments shallowly trilobed; the single siphon transversing adjacent segments is thick walled .....  
..... *H. cryptica*  
Segments bear resemblance to maple leaves; the single siphon transversing adjacent segments is thin walled .....  
..... *H. acerifolia*
10. Thalli attached by basal rhizoids ..... 11  
Thalli attached by often large, bulbous rhizoidal masses ..... 13
11. Segments usually less than 6.0 mm broad ..... *H. goreau*  
Segments usually more than 6.0 mm broad ..... 12
12. Plants frequently pendant over steep overhangs, segment surface slightly glossy; segments to 1.0 mm thick .....  
..... *H. copiosa* (in part)  
Plants frequently decumbent; segments to 2.0 mm thick ..... *H. gracilis*
13. Segments ribbed, frequently trilobed; surface utricles 42–84  $\mu$ m diam ..... *H. incrassata*  
Segments indistinctly ribbed or smooth; surface utricles 27–45  $\mu$ m diam ..... *H. simulans*

***Halimeda* sect. *Halimeda* J. V. Lamour.**

*Halimeda* sect. *Halimeda* J. V. Lamour. The section name, *Halimeda*, is an autonym (Turland et al. 2018: Articles 6.8, 22.3, 26.3).

Members possess medullary siphons that are mostly, partly, or completely fused in twos and threes, occasionally more, at the nodes. There are four taxa, three species, and one variety of *H.* sect. *Halimeda* recorded in Puerto Rico.

***Halimeda discoidea* Decne.**

FIGURE 44

*Halimeda discoidea* Decne. 1842a.

*Puerto Rican Records:* Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar 1964b; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution:* Belize, Costa Rica, Panama, North America, Bermuda, Bahamas, Antigua, Cuba, Jamaica, Nicaragua, Puerto Rico, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Unlikely “Kamtschatka” (Decaisne 1842a); “not certain” (Silva et al. 1996a). The herbarium label (PC) indicates collected “Kamtschatka” (formerly Russia) during the voyage of the exploring ship *Venus* (Decaisne 1842b: 102). The locality is incorrect as waters of the Kamchatka Peninsula (now Alaska) are far too cold for this tropical to subtropical species. Its exact type locality remains unknown (Hillis 1959; Hillis-Colinvaux 1980; Lipkin and Silva 2002; Norris 2010; Guiry and Guiry 2022).

Moderately calcified thalli are erect, 6.0–20 cm tall, and anchored by small dense clusters of rhizoids at the base. Basal segments are subterete; flattened and smooth upper segments are orbicular or suborbicular, measuring to 4.0 cm wide, 3.0 cm long, and 0.7–1.4 mm thick. Segments with entire margins become transversely oval to reniform with maturity. Plants are

sparingly dichotomously branched in one plane. Subcortical utricles are inflated, 50–260  $\mu\text{m}$  diam, bearing up to 14 peripheral truncate utricles, 30–90  $\mu\text{m}$  diam in surface view. Siphons more or less completely fuse in groups of twos and threes at the nodes. Algae are grayish green or whitish.

**Habitat and Comments:** *Halimeda discoidea* occurs on sandy bottoms in shallow water and is associated with coral reef environments. The species also grows at moderate depths to deep water. It is known to a maximum depth of 70 m in Puerto Rico (Ballantine et al. 2016). Segments of deeper-water specimens that conform to *H. discoidea* var. *platyloba* Børgesen (1911) measure to 3.0 cm across. The variety, however, is now regarded as synonymous with the nominate form. However, genetic analyses by Verbruggen et al. (2005) indicated that *H. discoidea* was composed of a complex of cryptic or overlooked species. *Halimeda discoidea* var. *platyloba* requires testing to elucidate its

phylogenetic relationships and taxonomic status. [Additional illustrations: Howe 1907: pl. 25: figs. 11–20, pl. 26; Norris 2010: fig. 48A–C; Littler et al. 2008: 224.]

***Halimeda hummii* D. L. Ballant.**

FIGURE 45

*Halimeda hummii* D. L. Ballant. 1982: 87–89, figs. 1–6, 10.

**Puerto Rican Records:** Ballantine 1982; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

**Western Atlantic Distribution:** Costa Rica, North America, Panama, Puerto Rico.

**Type Locality:** Edge of insular shelf offshore from La Parguera, Puerto Rico.

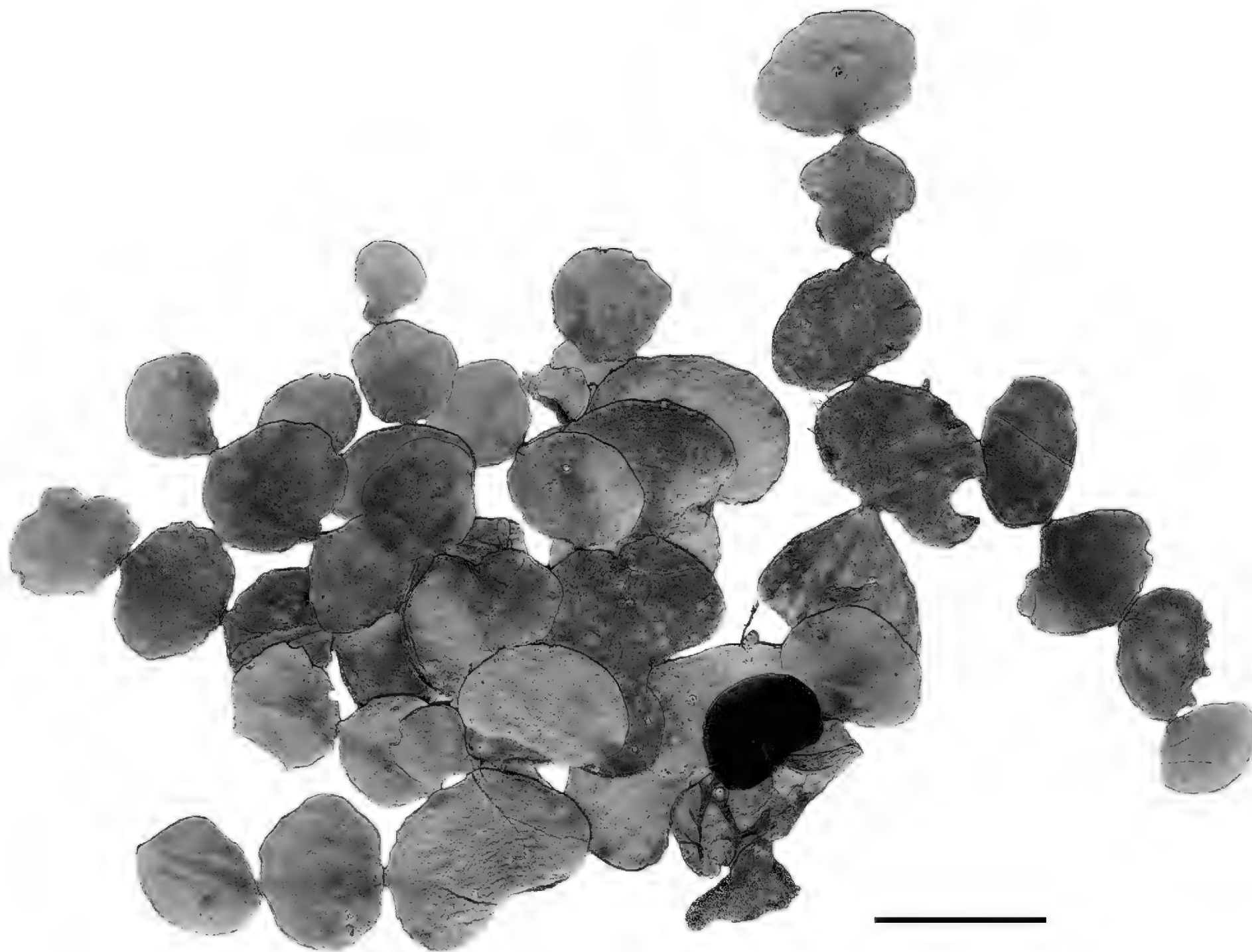


FIGURE 44. *Halimeda discoidea*. DLB8412, herbarium specimen: Algal plain, offshore from Punta Brea, 16 m. Scale bar = 2.0 cm.



FIGURE 45. *Halimeda hummii*. In situ habit photograph from edge of insular shelf offshore from Salinas, 20 m. Field = approximately 2.0 cm.



Moderately calcified thalli are short statured, to 25 mm tall, originating from a single holdfast. Branching is highly irregular with up to 4 branches originating from a single enlarged segment. Segments are quite variable in shape, ranging from cylindrical to flattened and irregular. Segments range from (0.2–)0.9 to 2.4(–3.5) mm wide and from (0.8–)1.3 to 2.3(–3.2) mm long. Upper segments average slightly greater dimensions than lower ones. Segment margins are entire to erose. Medullary siphons range from 30 to 80  $\mu$ m diam. The cortex consists of 1, 2, or, rarely, 3 series of utricles. Cortical utricles in surface view are sunken, giving the segment surface a pitted appearance. Outermost peripheral utricles are pentagonal or hexagonal, (30–)38–52(–62)  $\mu$ m diam in surface view, and remain attached after decalcification. Disposition of medullary filaments at the nodes is inconsistent, as they may pass through the node unfused or, as is generally the case, they fuse in pairs.

**Habitat and Comments:** *Halimeda hummii* has been collected at both offshore, shelf edge sites in southwestern Puerto Rico at 20 m depth and nearshore at Ballena Bay, Guánica at a depth of less than 2.0 m. More recently, it was collected in deep water from 62 m at “El Hoyo” and at 70 m at Vieques (Ballantine et al. 2016).

***Halimeda tuna* (J. Ellis et Sol.) J. V. Lamour.**

FIGURE 46

*Halimeda tuna* (J. Ellis et Sol.) J. V. Lamour. 1816: 309.

*Basionym:* *Corallina tuna* J. Ellis et Sol. 1786: 111, pl. 20e.

**Puerto Rican Records:** As *Halimeda tuna*: Taylor 1960; Almodóvar and Blomquist 1961; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

**Western Atlantic Distribution:** Belize, Costa Rica, Panama, North America, Bermuda, Bahamas, Anguilla, Antigua, Barbados, Cuba, Guadeloupe, Hispaniola, Jamaica, Martinique, Nicaragua, Puerto Rico, Saba Bank, St. Eustatius, St. Martin, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Mediterranean Sea.

*Halimeda tuna* is the generitype species. The lightly calcified thalli are 10–25 cm tall and are attached by a reduced rhizoidal tuft. The lowermost 1–2 segments comprise the stipe; these are subterete and fused. Above the stipe, segments are flat and cuneate to generally rounded, transversely oval to reniform. The segments measure to 2.0 cm wide and 1.0–3.0 cm long. Branching is in one plane. Cortical utricles occur in 2–4 layers. Peripheral utricles measure (25–)40–75(–125)  $\mu$ m diam in surface view and are 40–130  $\mu$ m long. Club-shaped subsurface utricles, 20–110  $\mu$ m diam and 40–120  $\mu$ m long, each bear 2–7 surface utricles. Medullary filaments fuse in groups of 2 or 3 at the nodes. Algae are dark green in color.

**Habitat and Comments:** *Halimeda tuna* is common on shallow-water reefs in Puerto Rico and occurs down to 70 m depths (Ballantine et al. 2016). Along with *H. incrassata* (J. Ellis) J. V. Lamour., *H. tuna* is one of the most common species in Puerto Rico. Elsewhere in the Caribbean it has been dredged from 32 to 80 m (Taylor 1960) and occurs in deep water in the Bahamas from 70 to 100 m depths (Blair and Norris 1988). *Halimeda tuna* f. *platydisca* (Decne.) E. S. Barton is no longer recognized as an entity different from the nominate species but possesses larger segments, to 4.0 cm broad.

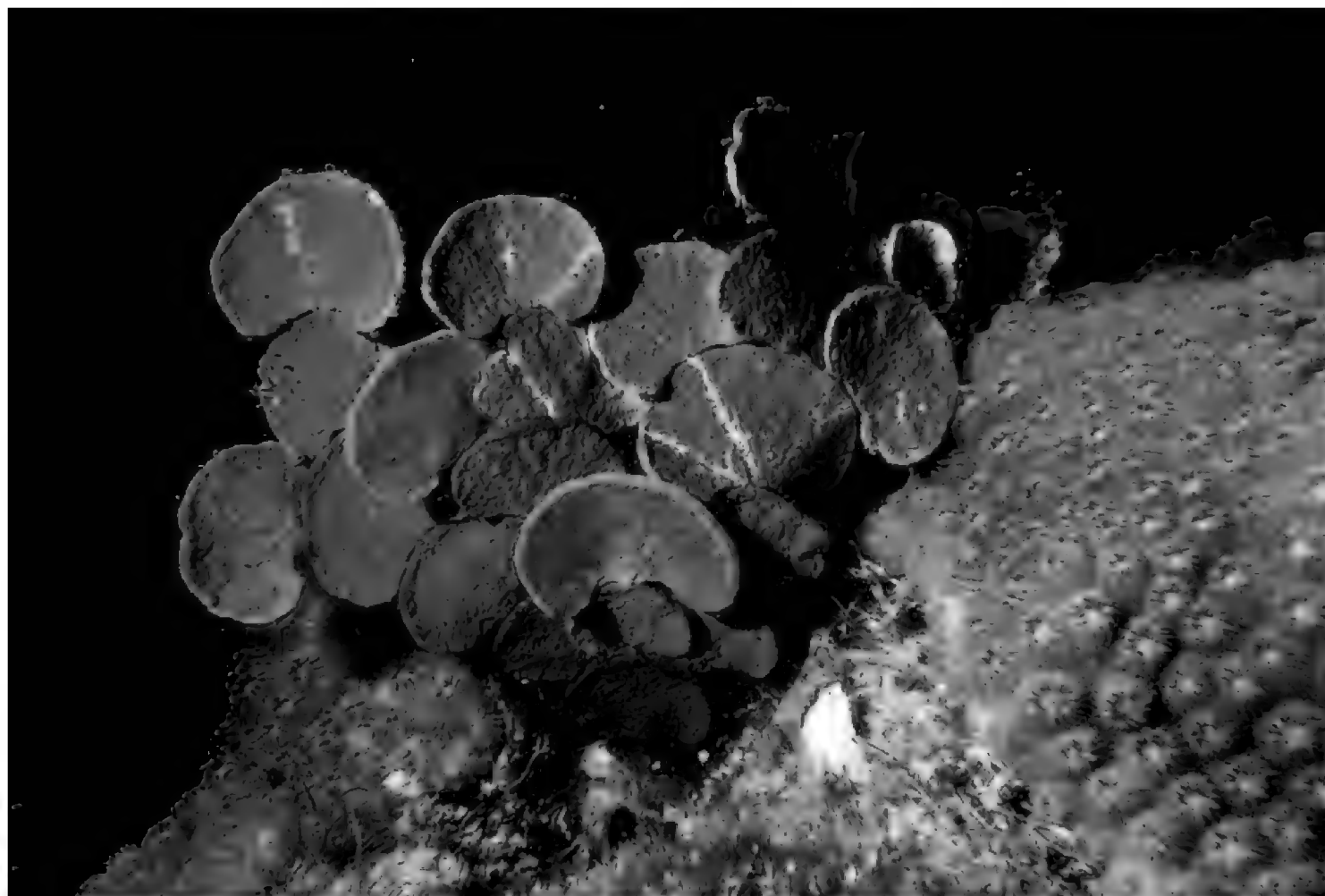


FIGURE 46. *Halimeda tuna*. In situ habit photograph from Laurel Reef, La Parguera, 5.0 m. Field = approximately 7.0 cm.



Meinesz (1980: 124) suggested the Mediterranean *Pseudochlorodesmis furcellata* (Zanardini) Børgesen (1925: fig. 34; generitype) may be the juvenile form of *H. tuna*; however, the genus *Pseudochlorodesmis* Børgesen (1925) is currently accepted as a member of the Udoteaceae (Kraft 2007; Guiry and Guiry 2022). [Additional illustrations: Harvey 1858: pl. 40A; Barton 1901: pl. 1, fig. 1; Taylor 1960: pl. 24: fig. 5; Blair and Norris 1988: figs. 8–9; Braune and Guiry 2011: fig. 21.7.]

### ***Halimeda* sect. *Crypticae* Hillis-Col. sensu stricto**

*Halimeda* sect. *Crypticae* Hillis-Col. 1980: 86.

Thalli of *H. sect. Crypticae* sensu stricto possess a single central medullary siphon, running from the base through nodes and segments to the apex. Thalli grow on hard substrata, such as rock or dead coral, and are attached by a holdfast of rhizoidal filaments.

**Notes:** Three species of *H. sect. Crypticae* occur in Puerto Rico: *Halimeda cryptica* Hillis-Col. et E. A. Graham; *H. pumila* Verbruggen, D. S. Littler, et Littler; and *H. acerifolia* comb. nov. *Halimeda pumila* and *H. acerifolia* (newly recognized herein) are deepwater species, apparently restricted to the Caribbean. The phylogenetic analyses of Verbruggen et al. (2007) and Pongparadon et al. (2015) aligned *H. cryptica* in the same lineage as the tropical Pacific *H. micronesica* Yamada (1941), the type of *H. sect. Micronesicae* (Verbruggen and Kooistra 2004). The two sections primarily differ only in morphology: *H. sect. Crypticae* has a single (central) medullary siphon throughout and surface utricles that remain adhered to each other after decalcification; *H. sect. Micronesicae* has more than 1 medullary siphon that is completely separated or slightly joined (but not fused) at the nodes and surface utricles that separate after decalcification. *Halimeda pumila* specimens may display both conditions. The section also originally included species in which several medullary siphons pass through nodal regions without fusing.

Verbruggen et al. (2007) expanded the criteria to include species in which 1 or more unfused medullary siphons pass through the nodes. In so doing, *Halimeda* sect. *Crypticae* was subsumed. We have chosen to recognize *H. sect. Crypticae* sensu stricto.

### ***Halimeda acerifolia* (D. L. Ballant.) D. L. Ballant. et J. N. Norris comb. nov. et stat. nov.**

FIGURE 47

*Halimeda acerifolia* (D. L. Ballant.) D. L. Ballant. et J. N. Norris comb. nov.  
et stat. nov.

**Basionym:** *Halimeda cryptica* var. *acerifolia* D. L. Ballant. 1982: 89,  
figs. 7–9, 11.

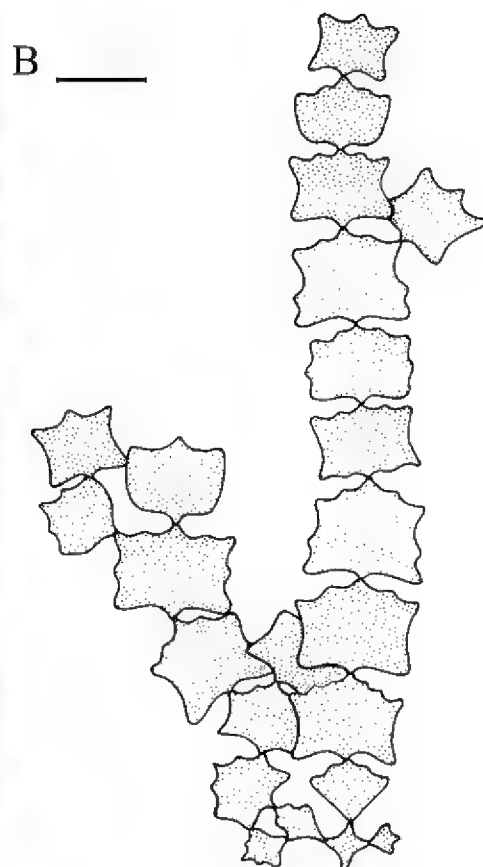
**Puerto Rican Records:** As *Halimeda cryptica* var. *acerifolia*:  
Ballantine 1982; Ballantine et al. 2016.

**Western Atlantic Distribution:** Bahamas, Cuba(?), Martinique,  
Puerto Rico.

**Type Locality:** Edge of insular shelf, offshore from Salinas,  
Puerto Rico.

Thalli are erect, measuring to 5.0 cm tall, composed of firmly calcified, extremely fragile, and brittle segments. Branching is sparse and mostly dichotomous or trichotomous in one plane, above a single short stalk. Lowermost basal segments are small and trilobed, 3.0–5.0 mm wide, 3.0–4.0 mm long. Upper segments are larger and flat, 8.0–12 mm wide and 5.0–8.0 mm long. Segments possess a short conical stalk at the center of their lower margins, and the distinctively shaped mature segments are highly dentate on their upper margins, entire segments resembling maple leaves.

A single, central medullary siphon, 100–210 µm diam, is continuous from the lowermost segment to the apex. The medullary



**FIGURE 47.** *Halimeda acerifolia*. (A) In situ habit photograph from edge of insular shelf offshore from La Parguera, 60 m, Field = approximately 2.0 cm. (B) DLBsn, drawn from the holotype: Edge of insular shelf, offshore from Margarita Reef, La Parguera, 91 m. Scale bar = 1.0 cm.

filament branches trichotomously near the base of each daughter segment. The cortex is made up of 2 layers of utricles, constricted at their forks; they terminally bear 4–6 cortical utricles. In surface view, cortical utricles measure (33–)44–67(–88)  $\mu\text{m}$  diam.

*Halimeda acerifolia* was originally described as a variety of *H. cryptica*, principally on the basis of both entities having the then unique character of a single medullary siphon running through adjacent segments. However, *H. acerifolia* and *H. cryptica* differ in other morphological characters. *Halimeda acerifolia* is distinguished by its large, single medullary siphon that lacks wall thickenings at the nodes and distinct trilobed segments of the single basal segment and lowermost segments. Aside from its distinctively shaped segments, *Halimeda acerifolia* differs from *H. cryptica* in its height, smaller segment size, fewer utricles layers, and smaller diameter of surface utricles. Plant height in *H. acerifolia* is to 5.0 cm tall versus to 10 cm in *H. cryptica*. Segments in *H. acerifolia* are 8.0–12 mm wide and 5.0–8.0 mm long versus 15 mm wide and 11 mm long; cortical utricles in surface view are 44–67  $\mu\text{m}$  versus 56–76  $\mu\text{m}$ . *Halimeda acerifolia* possesses 2 layers of cortical utricles, whereas *H. cryptica* possesses 2–3(–4) layers of cortical utricles.

**Habitat and Comments:** *Halimeda acerifolia* is rarely encountered in the Caribbean and in Puerto Rico. The species occurs only in deepwater habitats, 53–70 m depths (Ballantine et al. 2016). Nevertheless, Guimaraes Bermejo et al. (2009) reported the new species as *H. cryptica* var. *acerifolia* from very shallow water (less than 1.0 m deep) in a mangrove channel. [Additional illustration: Guimaraes Bermejo et al. 2009: fig. 2.]

### ***Halimeda cryptica* Hillis-Col. et E. A. Graham**

FIGURE 48

*Halimeda cryptica* Hillis-Col. et E. A. Graham in Colinvaux and Graham 1964: 6, pls. 3–6.

**Puerto Rican Records:** Ballantine 1982; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

**Western Atlantic Distribution:** Bahamas, Jamaica, Puerto Rico, Martinique.

**Type Locality:** Off Cardiff Hall beach, Runaway Bay, St. Ann Parrish, Jamaica.

Thalli are up to 10 cm tall, pendant or tangled, with dichotomous or trichotomous branching above an abbreviated holdfast. The basal segment is singular and turbinate with the lower half of its margin deeply incurved. Segments are strongly calcified and brittle. Upper segments are broadly ovate, to 11 mm long, 15 mm broad, and 0.33–0.66 mm thick. The segment upper margins are shallowly trilobed, and the lower margins are auriculate to truncate. A single thick-walled medullary filament passes between the segments at nodal regions. Utricles, (42–)54–69(–83)  $\mu\text{m}$  long, occur in 2–3(–4) layers with peripheral utricles remaining mostly attached after decalcification, measuring (36–)56–76(–103)  $\mu\text{m}$  diam in



FIGURE 48. *Halimeda cryptica*. DLBsn, herbarium specimen: Edge of insular shelf, offshore from Margarita Reef, collected by C. Arneson, 91 m. Scale bar = 1.0 cm.

surface view. Algae are light green to off white on exposed surfaces, and the shaded surface is whitish.

**Habitat and Comments:** In Puerto Rico *Halimeda cryptica* occurs on the reef slope of the edge of insular shelf at 70–82 m depths, off the south coast seaward of Margarita Reef between La Parguera and the Cabo Rojo lighthouse (Ballantine 1982; Ballantine et al. 2016). Originally, *H. cryptica* was reported in Jamaica from 25 to 65 m depths and since then was reported down to 152 m in the Bahamas from San Salvador Island (Blair and Norris 1988).

### ***Halimeda pumila* Verbruggen, D. S. Littler, et Littler**

FIGURE 49

*Halimeda pumila* Verbruggen, D. S. Littler, et Littler 2007: 516, figs. 1 (middle), 2 (lower left), 3 (upper right), and 4 (middle).

**Puerto Rican Records:** Ballantine et al. 2011a, 2016.

**Western Atlantic Distribution:** Bahamas, Cuba(?), Puerto Rico.

**Type Locality:** Off SW side of San Salvador Island, Bahamas.

Thalli are small, measuring to 2.0 cm tall, and are sparsely branched in one plane. The segments are heavily calcified and

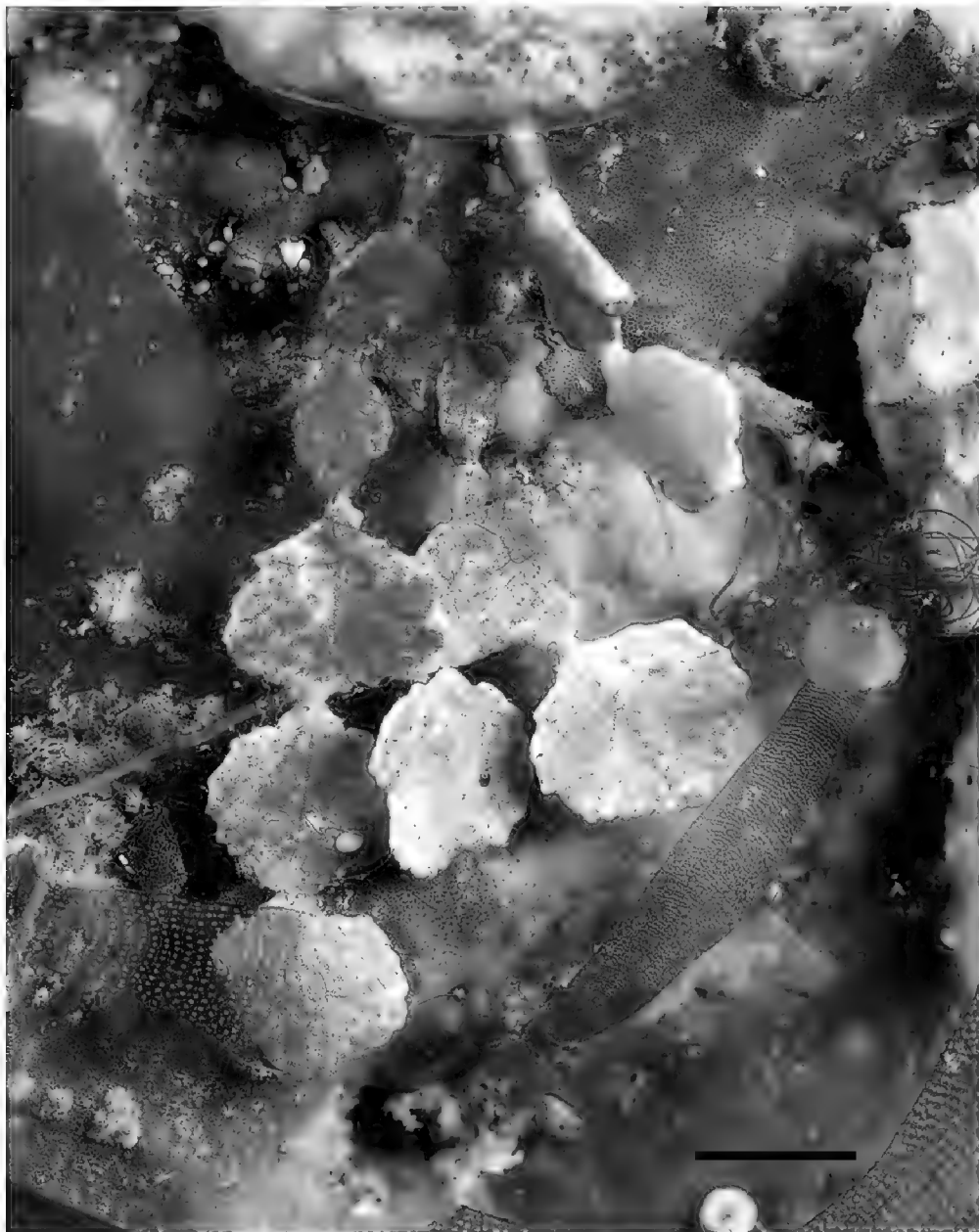


FIGURE 49. *Halimeda pumila*. DLB7867: Edge of insular shelf, La Parguera, 82 m. Scale bar = 2.0 mm.

brittle, (1.6–)2.4(–3.0) mm wide, (1.6–)2.0(–3.2) mm long, and approximately 160  $\mu\text{m}$  thick. Most segments are slightly wider than long and broadest just above their middle; the upper margins are slightly crenate, and the lower margins are generally smoothly rounded. Lateral branches are initiated from the broadest segment portion. A single central siphon or as many as 3, measuring (70–)80–95(–115)  $\mu\text{m}$  diam, transverse the nodes between adjacent segments. There are 2 layers of cortical utricles. The peripheral utricles are irregularly polygonal, (20–)25–35(–40)  $\mu\text{m}$  in surface diam and (20–)25–30(–40) mm in length. Subperipheral utricles are (8.0–)10–20(–25)  $\mu\text{m}$  diam and (10–)15–35(–50)  $\mu\text{m}$  long.

**Habitat and Comments:** The intact Puerto Rican specimens of *H. pumila* were only 6 segments long with 1 branch. Three medullary filaments, 40–50  $\mu\text{m}$  diam, transverse the node. Although the Bahamian (type) *H. pumila* normally has a single medullary siphon passing through the nodes, Verbruggen et al. (2007) noted that in some cases, 3 unfused siphons pass through the nodes (see Verbruggen et al. 2007: fig. 2, lower left). The lack of a strict nodal development pattern was invoked by Verbruggen et al. (2007) as support for placement of the species in *H. sect. Micronesicae*. Because of its rarity, Verbruggen et al.

(2007) were unable to obtain molecular sequence data for *H. pumila*. Its definitive sectional affiliation will probably not be resolved until it can be molecularly analyzed.

Apparently rare, only two specimens of *Halimeda pumila* are known in Puerto Rico, both from deep water (59–82 m depths) and attached beneath the growing edge of *Peyssonnelia flavescens* D. L. Ballant. et H. Ruiz (Ballantine et al. 2016). The report of *H. pumila* collected in a mangrove channel in water less than 1.0 m deep (Guimaraes Bermejo et al. 2009) is surprising, and specimens should be reexamined. [Additional illustration: as *Halimeda cryptica* var. *acerifolia*, Littler and Littler 2000: 401 (photograph of the holotype in situ).]

### ***Halimeda* sect. *Opuntiae* J. Agardh ex De Toni**

*Halimeda* sect. *Opuntiae* J. Agardh ex De Toni 1889: 521.

Type Species: *Halimeda opuntia* (L.) J. V. Lamour. 1816: 308.

Species of the subdivision *H. sect. Opuntiae* have medullary siphons partially fused over a short distance at the nodes between calcified segments. Two species and one form of *H. sect. Opuntiae* occur in Puerto Rico.

### ***Halimeda goreau* W. R. Taylor**

FIGURE 50

*Halimeda goreau* W. R. Taylor 1962b: 173, figs. 1–7.

**Puerto Rican Records:** Almodóvar and Blomquist 1965; Ballantine 1977; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

**Western Atlantic Distribution:** Belize, Panama, North America, Bahamas, Barbados, Cuba, Jamaica, Puerto Rico, Colombia.

**Type Locality:** About 30 m depth; Cardiff Hall beach, St. Ann Parish, Jamaica.

Thalli, to 13 cm tall, are attached by rhizoidal tufts. Segments strongly calcified proximally are less calcified distally. The lower segments are cylindrical to subcuneate, and upper segments are trilobed or deltoid, 2.5–6.0 mm wide, 3.0–4.0 mm long, and 300–500  $\mu\text{m}$  thick. Segment faces are nitent, often slightly ribbed. Branching is in one plane. Medullary siphons are fused in pairs between segments. Utricles occur in 3–6 layers with peripheral utricles measuring 15–37  $\mu\text{m}$  diam in surface view and 15–45  $\mu\text{m}$  long. Subsurface utricles are smaller, 10–30  $\mu\text{m}$  diam and 20–60  $\mu\text{m}$  long. Algae are bright green in color.

**Habitat and Comments:** In Puerto Rico, *Halimeda goreau* is extremely common at the insular shelf edge break at 18 m depth, offshore from La Parguera, becoming less abundant with depth, having been collected to a maximum of 73 m (Ballantine et al. 2016). In Jamaica *H. goreau* was reported in shallow water at 3.6 m, but mostly occurred deeper, from 22 to 46 m





FIGURE 50. *Halimeda goreauui*. In situ habit photograph from the edge of the insular shelf offshore from La Parguera, 20 m. Field = approximately 0.5 m.

depths (Taylor 1962b). In the Bahamas the species is also known from 29 to 61 m depths off San Salvador Island (Blair and Norris 1988) and on the east coast reefs off the northern Florida Keys from 20 to 80 m depths (Lirman and Biber 2000). [Additional illustrations: Littler and Littler 2000: 402.]

***Halimeda opuntia* (L.) J. V. Lamour. f. *opuntia***

FIGURE 51A

*Halimeda opuntia* (L.) J. V. Lamour. 1816: 308.

*Basionym*: *Corallina opuntia* L. 1758: 805.

*Puerto Rican Records*: Almodóvar and Blomquist 1965; Ballantine 1977; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution*: Belize, Panama, North America, Bahamas, Barbados, Cuba, Jamaica, Puerto Rico, Colombia.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Jamaica fide Hillis (1959; Hillis-Colinvaux 1980).

Thalli extend laterally to form large, spreading colonies, to 1.0 m in extent, with clumps to 50 cm high. Thalli attach at multiple points, with no persisting primary base or axis; plants are densely branched in multiple planes. Transversely oval to reniform segments are strongly calcified, possessing truncate lower margins. The segments may be contorted, commonly with 3 radiating ribs; the segments measure 7.0–20 mm wide and 4.5–12 mm long. Surface utricles measure (12–)20–50(–63)  $\mu\text{m}$  diam and 15–30(–70)  $\mu\text{m}$  long. The medullary filaments are generally incompletely fused in pairs at the nodes. Algae are deep green to whitish green in color.

**Habitat and Comments:** *Halimeda opuntia* is, perhaps, the most easily recognized of the Puerto Rican *Halimeda* species. It is very abundant in a variety of habitats, forming large growths of compact growths on shallow, exposed reef flats, in sheltered seagrass beds, and occasionally in deeper water, to 55 m depth. *Halimeda opuntia* has been characterized as a species complex of several cryptic, misidentified, or unknown species (e.g., Verbruggen et al. 2005). [Additional illustrations: Harvey 1858: pl. 40B; Barton 1901: pl. 2, fig. 19; Huisman 2015: fig. 28C–E.]

***Halimeda opuntia* f. *triloba* (Decne.) J. Agardh**

FIGURE 51B

*Halimeda opuntia* f. *triloba* (Decne.) J. Agardh 1887: 84.

*Basionym:* *Halimeda triloba* Decne. 1842a: 102.

**Puerto Rican Records:** Herein reported as new record from Puerto Rico: LRAsn, Bahía Fosforescente, La Parguera, Lajas (23.I.1975, US Alg. Coll. 219157).

**Western Atlantic Distribution:** Panama, North America, Cuba, Guadeloupe, Jamaica, Netherlands Antilles, Puerto Rico, Brazil.

**World Distribution:** See Guiry and Guiry (2022).

**Syntype Localities:** “In Oceano indico, [and] Manillá” (Decaisne 1842a: 102); note that later, “Oceano indico” was given as Ceylon by J. Agardh (1887).

**Lectotype Locality:** China Sea fide Barton (1901: pl. II, fig. 20; see Silva et al. 1996: 871).

Thalli are irregularly branched, of loose (not dense) scattered branches, forming large clumps or mounds, anchored by rhizoidal

attachments where in contact with substratum. Branching is random or sometimes in one plane at right angles to the adjacent segment. Segments are heavily calcified and flattened, with distinctive, often deeply trilobed upper margins and flat to contorted, ribbed surfaces, up to 11 mm broad, 7.0 mm long, and 0.5–1.2 mm thick.

**Habitat and Comments:** *Halimeda opuntia* f. *triloba* occurs in seagrass beds. Although it has not always been considered a separate taxon, we are in agreement with those who recognize two forms (e.g., Taylor 1960; Dawes 1974; Littler and Littler 2000; Wynne 2005, 2017; Dawes and Mathieson 2008). Pongparadon et al. (2015) addressed morphological variation in *H. opuntia* with respect to environmental influence. Under high-irradiance conditions, *H. opuntia* colonies are compact, possessing reniform-shaped segments, and under low-light conditions, colonies are more loosely organized with deeply trilobed segments. *Halimeda opuntia* f. *triloba* conforms to Pongparadon et al.’s (2015) figures of *H. opuntia* grown under regimes of lower light irradiance. [Additional illustrations: as *Halimeda triloba*, Kützting 1858: 9, pl. 22: fig. 3 (illustration of the type); Barton 1901: pl. 2, fig. 20.]

***Halimeda* sect. *Pseudo-opuntiae* J. Agardh ex De Toni**

*Halimeda* sect. *Pseudo-opuntiae* J. Agardh ex De Toni 1889: 520.

*Lectotype Species:* *Halimeda gracilis* Harv. ex J. Agardh 1887: 82.

*Halimeda* sect. *Pseudo-opuntiae* encompasses the species of *Halimeda* that have club-shaped, subsurface cortical utricles. There is single species of the section known in Puerto Rico.

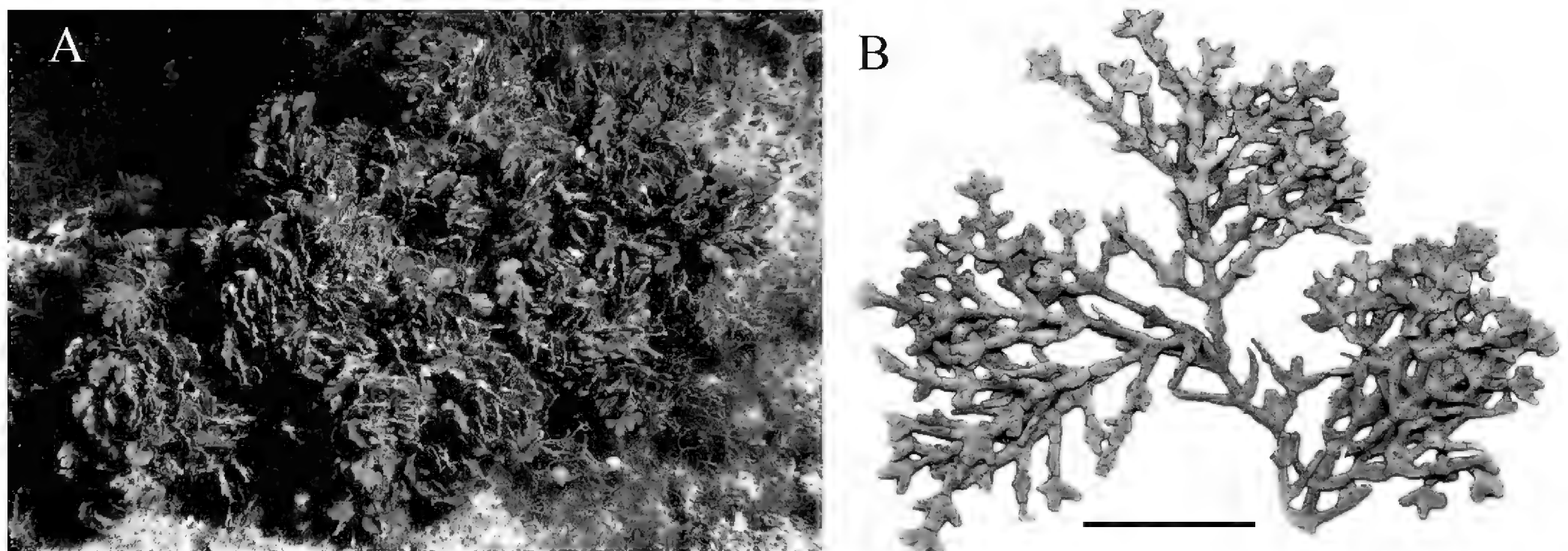


FIGURE 51. *Halimeda opuntia*. (A) *H. opuntia* f. *opuntia*. In situ habit photograph from El Mario Reef, La Parguera. Field = approximately 20 cm. (B) *H. opuntia* f. *triloba*. LRAsn, herbarium specimen: Bahia Fosforescente, La Parguera. Scale bar = 2.0 cm.



***Halimeda gracilis* Harv. ex J. Agardh**

FIGURE 52

*Halimeda gracilis* Harv. ex J. Agardh 1887: 82.*Puerto Rican Records:* Taylor 1960; Ballantine 1982; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.*Western Atlantic Distribution:* Belize, Panama, North America, Bahamas, Barbados, Cuba, Jamaica, Puerto Rico, St. Eustatius, U.S. Virgin Islands, Brazil.*World Distribution:* See Guiry and Guiry (2022).*Type Locality:* “In oceano Indico ad Ceylonam” (Agardh 1887: 82); Sri Lanka, Indian Ocean.

Thalli are erect or decumbent in habit, reaching to 40 cm in extent. Algae are attached by basal rhizoidal masses and rhizoids from decumbent segments in contact with substrata. Segments are substantially calcified proximally, somewhat less above. In shape, segments are subterete proximally and cuneate to subreniform distally. They are not ribbed, and the margins are slightly undulate, measuring 1.5–15 mm wide, 0.5–9.0 mm long, and 0.5–2.0 mm thick. Branching is irregular, with up to 5 branches originating from a single segment. The cortex possesses 2(–3) utricle layers. Subsurface utricles are club shaped, swollen or flattened distally, 20–125  $\mu\text{m}$  diam and 100–400  $\mu\text{m}$  long. Peripheral utricles measure (23–)30–45(–70)  $\mu\text{m}$  diam in surface view and are 40–110

$\mu\text{m}$  long. Medullary filaments are completely fused in pairs, sometimes in threes at the nodes and trichotomously divided above the nodes. Algae are light green in color.

*Habitat and Comments:* In Puerto Rico, *Halimeda gracilis* is mostly found in deeper waters on sand plains, 55–70 m depths (Ballantine et al. 2016), and rarely in habitats shallower than 17 m. Elsewhere in the western Atlantic, *H. gracilis* occurs from 40 to 60 m depths in the Florida Keys (Leichter et al. 2008) and down to 152 m depths off San Salvador Island (Blair and Norris 1988). Phylogenetic analysis by Dijoux et al. (2012) revealed a tree including four separate clades of specimens identified as “*Halimeda gracilis*.” One clade included the type locality (Sri Lanka) of *H. gracilis*, and two other clades included “*H. gracilis*” from different Atlantic locales, suggesting that *Halimeda gracilis* is actually a species complex. Caribbean specimens referred to the species require molecular comparisons to elucidate their phylogenetic relationship and taxonomic status. [Additional illustrations: Barton 1901: pl. 3, fig. 28; Blair and Norris 1988: fig. 6.]

***Halimeda* sect. *Rhipsalis* J. Agardh ex De Toni***Halimeda* sect. *Rhipsalis* J. Agardh ex De Toni 1889: 523*Lectotype Species:* *Halimeda incrassata* (J. Ellis) J. V. Lamour. 1816: 307.

*Halimeda* sect. *Rhipsalis* encompasses species of *Halimeda* that have medullary siphons with pores connecting siphons at nodes, completely fused together into a single bundle between

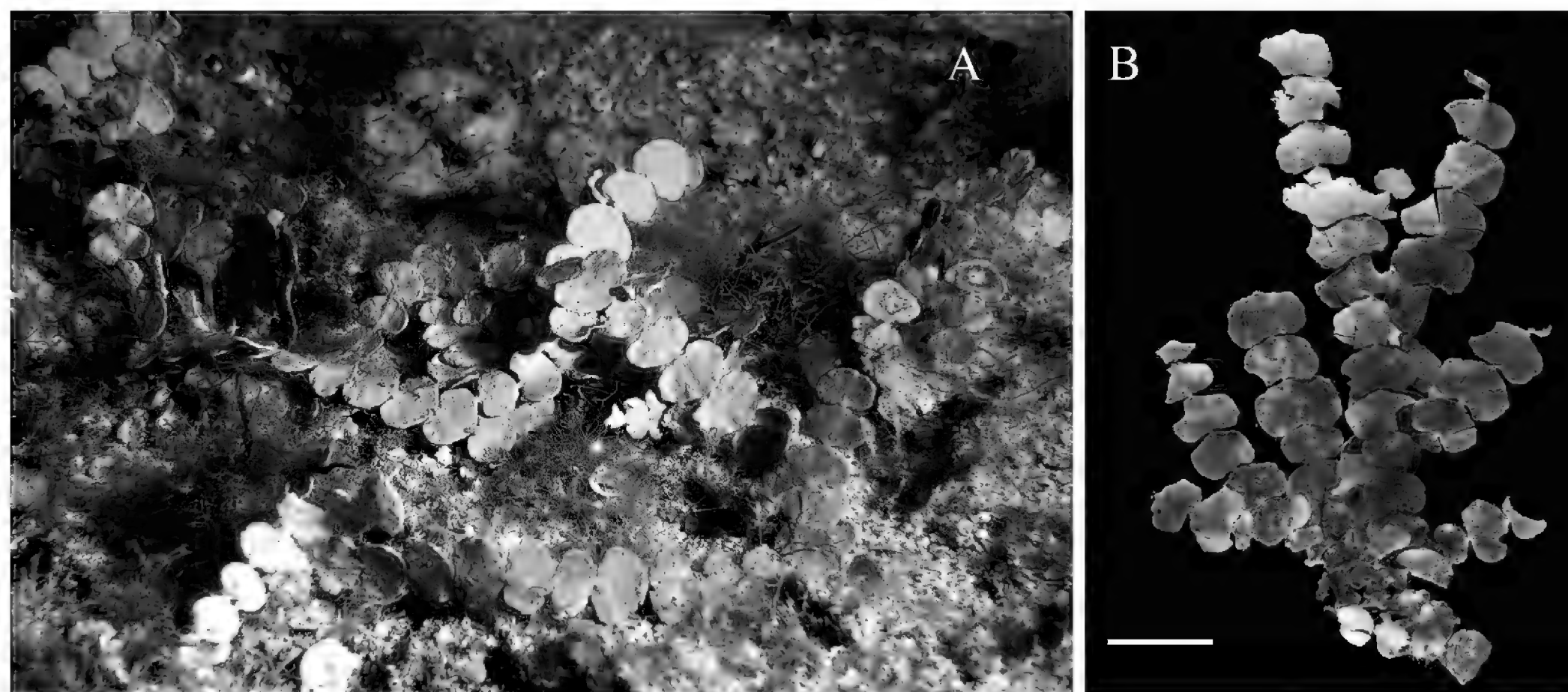


FIGURE 52. *Halimeda gracilis*. (A) In situ habit photograph, seaward Margarita Reef, 24 m. Field = approximately 20 cm. (B) Detail of plant. Scale bar = 2.0 cm.

the segments, and segments fused in the basal portion of the thallus. There are four species and one form known in Puerto Rico.

***Halimeda copiosa* Goreau et E. A. Graham**

FIGURE 53

*Halimeda copiosa* Goreau et E. A. Graham 1967: 433, figs. 1–10.

*Puerto Rican Records:* Taylor 1960; Ballantine 1982; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution:* Belize, Panama, North America, Bahamas, Barbados, Cuba, Jamaica, Puerto Rico, St. Eustatius, U.S. Virgin Islands, Brazil.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Jamaica.

Thalli, frequently pendant, reaching to 70 cm long from a single small holdfast. Algae are bushy to lax with ditrichotomous branching in one plane. Segments are moderately to heavily calcified and ribbed. The proximalmost segments, and often the proximal branch segments, are small, trilobed, terete, or rhombic. Segments above are transversely oblong to ovate with entire upper margins, rarely lobed or crenate. Segments possess a truncate to cordate lower margin. Segments are usually largest in the middle third of a plant, measuring to 13 mm long and 21 mm broad, and are 0.3 to 1.0 mm thick when dried. The cortex usually possesses 3 utricle series. The outer utricles are hexagonal, measuring (27–)30–36(–40)  $\mu\text{m}$  in surface view, and are (26–)32–41(–48)  $\mu\text{m}$  long. Secondary utricles each support 4–6 cortical utricles, (25–)28–47(–63)  $\mu\text{m}$ , broad, narrowing slightly at the base. Medullary filaments fuse briefly in twos and threes at the nodes, rarely 5 together. The fused groups are lightly attached and little entangled. Algae are bright green when alive and gray green to greenish white when dried. The surface is slightly glossy.

*Habitat and Comments:* *Halimeda copiosa* is known to a depth of 100 m in Puerto Rico (Ballantine et al. 2016), and Ballantine and Aponte (2003) reported the species to a maximum depth of 107 m in the Bahamas, where it commonly forms long, pendant chains hanging from shelf wall ledges (see illustration by Suárez et al. 2015: 179, fig. 195). Blair and Norris (1988) commented that *H. copiosa* was the most common *Halimeda* species in the deepwater algal community at San Salvador, where they indicated a maximum depth of 152 m. Although usually a deepwater species, *H. copiosa* has also been reported at 10 m depths (Littler and Littler 2000). [Additional illustrations: Goreau and Graham 1967: 433, figs. 1–10; Blair and Norris 1988: figs. 2–3; Littler and Littler 2000: 399, fig. 3.]

***Halimeda incrassata* (J. Ellis) J. V. Lamour.**

FIGURE 54

*Halimeda incrassata* (J. Ellis) J. V. Lamour. 1816: 307.

*Basionym:* *Corallina incrassata* J. Ellis 1768: 408, pl. XVII, figs. 20–27.

*Heterotypic Synonym:* *Halimeda tridens* (J. Ellis et Sol.) J. V. Lamour. 1812: 186.

*Puerto Rican Records:* As *Halimeda incrassata*: Taylor 1960; Almodóvar and Pagán 1971; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002. As *Halimeda tridens*: Howe 1915; Almodóvar and Blomquist 1959, 1961.

*Western Atlantic Distribution:* Belize, Mexico, Panama, North America, Bermuda, Bahamas, Anguilla, Barbados, Cayman Islands, Cuba, Dominica, Grenadines, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Puerto



FIGURE 53. *Halimeda copiosa*. DLB7140, herbarium specimen: Bajo de Sico, Mayagüez, 50 m. Scale bar = 2.0 cm.

Rico, St. Barthélemy, St. Eustatius, St. Martin, Turks and Caicos, U.S. Virgin Islands, Brazil, Columbia, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* West Indies. The holotype is apparently lost (Barton 1901; Hillis-Colinvaux 1980). Lectotype selected by Verbruggen et al. (2006: 354).

Erect thalli, to 15–25 cm tall, arise from a massive bulbous base of rhizoids and sand. The upper thalli are strongly calcified. Lower segments of the alga form an extensive stalk composed of more or less terete segments that are fused, to 8.0 mm diam. Above the stalk, segments are flattened, triangular to ovate, often 3-lobed, sometimes more or less entire, usually with prominent vertical ribs. The segments are 4.0–14 mm wide, 3.0–10 mm long, and 0.7–2.0 mm thick. Branching is dichotomous. Utricles occur in 2–3 layers; the peripheral utricles are irregularly polygonal with rounded corners, measuring measure (34–)42–84(–105)  $\mu\text{m}$  diam in

surface view and are 55–90  $\mu\text{m}$  long. Medullary filaments are closely connected in a single group at the nodes (individual siphons cannot be separated) in an adhesion belt, 33–53  $\mu\text{m}$  in length, with many pores connecting to adjacent siphons (seen in dissection; Verbruggen et al. 2006: figs. 44–45). Algae are bright to dull green in color.

*Habitat and Comments:* The distribution of *Halimeda incrassata* is limited to the tropical western Atlantic (Verbruggen et al. 2006). In Puerto Rico, *H. incrassata* is extremely common in sandy habitats, inshore seagrass beds, and mangroves, as well as being a predominant member of the algal flora on offshore sand plains of Media Luna and Margarita Reefs. [Additional illustrations: as *Corallina incrassata*, Ellis and Solander 1786: pl. 20, figs. d1–d3, D1–D6; as *Halimeda tridens*, Harvey 1858: pl. 44C; as *Halimeda incrassata*, Barton 1901: pl. 4, fig. 39; Hillis-Colinvaux 1980: 20 (additional illustrations of Ellis 1768: pl. XVII: figs. 20–27); Verbruggen et al. 2007: figs. 27–31, 44–45, 55–56, 65–66; Littler et al.: 225.]

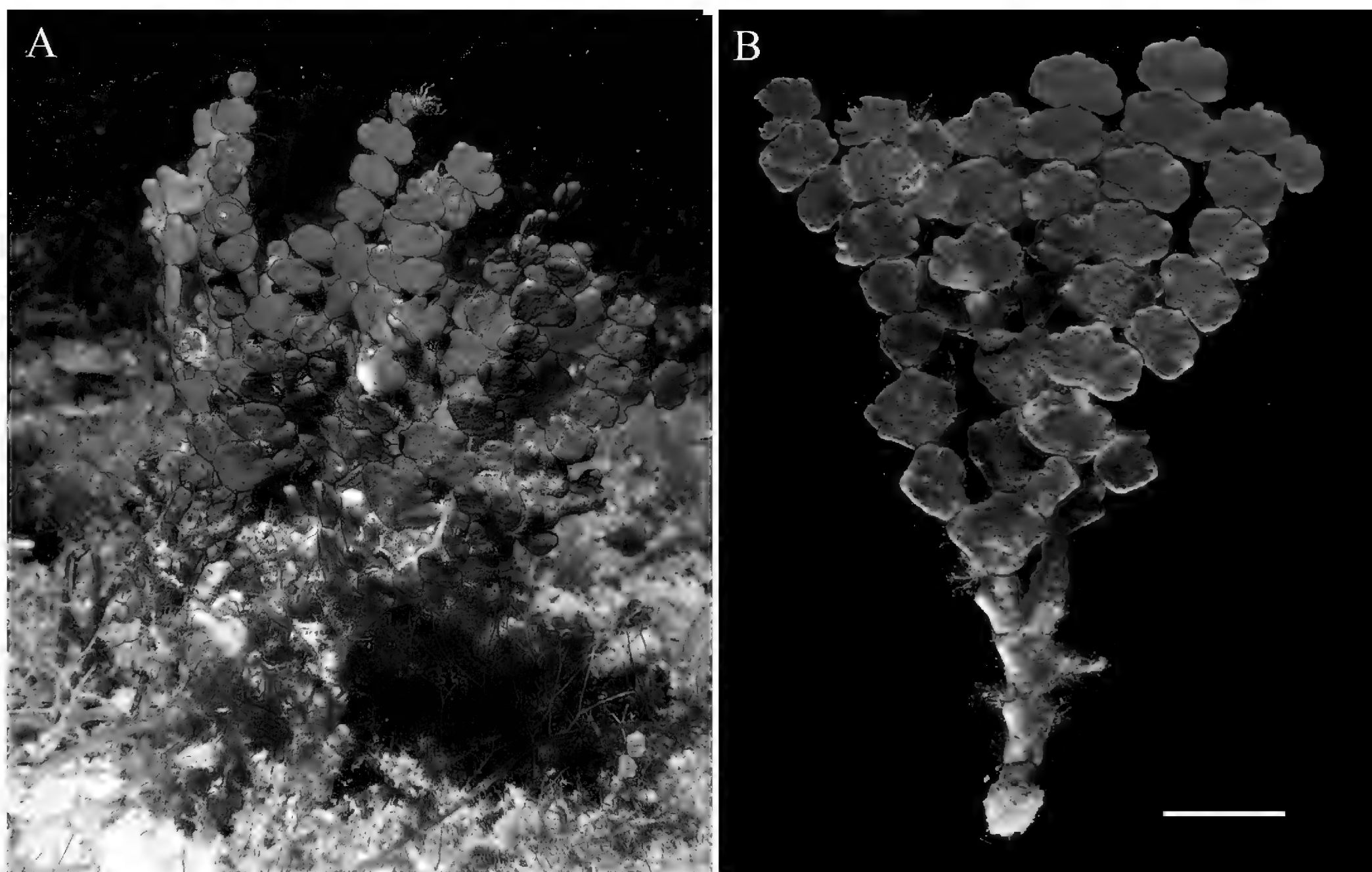


FIGURE 54. *Halimeda incrassata*. (A) In situ habit photograph from algal plain, seaward of Media Luna Reef, 17 m. Field = approximately 15 cm. (B) Detail of plant. Scale bar = 2.0 cm.



***Halimeda monile* (J. Ellis et Sol.) J. V. Lamour.**

FIGURE 55

*Halimeda monile* (J. Ellis et Sol.) J. V. Lamour. 1816: 306.

*Basionym*: *Corallina monile* J. Ellis et Sol. 1786: 110, pl. 20c.

*Homotypic Synonym*: *Halimeda incrassata* f. *monilis* (J. Ellis et Sol.) Barton 1901: 27, pl. 4, fig. 40.

*Puerto Rican Records*: As *Halimeda monile*: Howe 1915; Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar 1962,

1964a, 1964b; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution*: Belize, Mexico, Panama, North America, Bermuda, Anguilla, Antigua, Cayman Islands, Cuba, Guadeloupe, Hispaniola, Jamaica, Netherlands Antilles, Puerto Rico, St. Eustatius, Turks and Caicos, U.S. Virgin Islands, Colombia, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Jamaica.

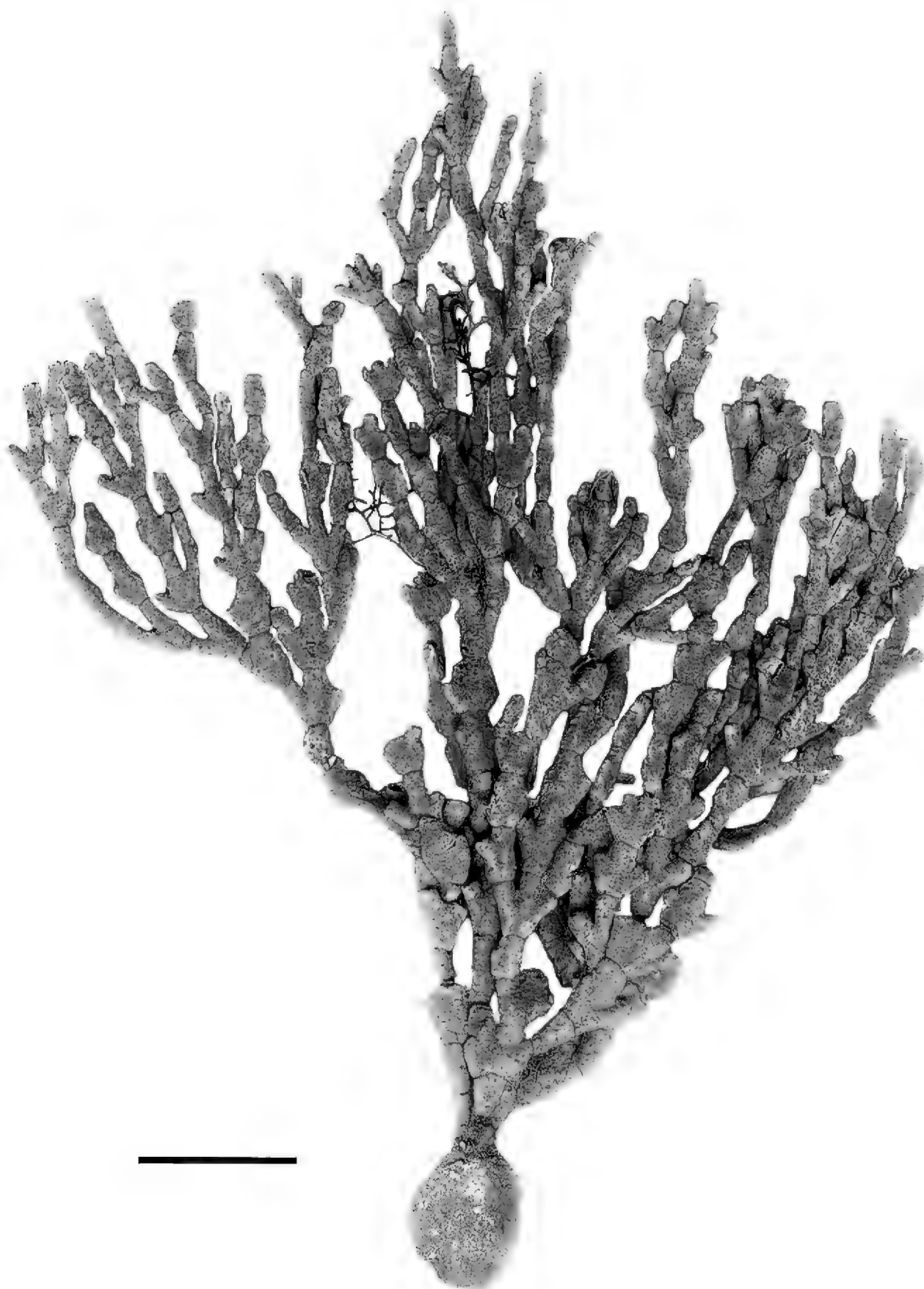


FIGURE 55. *Halimeda monile*. DLBsn, herbarium specimen: Punta Arena, Vieques Island, 1.0 m. Scale bar = 2.0 cm.



Erect thalli, 10–25 cm tall, are attached by a substantial base of rhizoids and sand. Segments are firmly calcified; the lowermost segments are flat and fused to form stipes or multiple axes issue from the holdfasts without stipes. Algae are closely branched above at narrow angles with disc-shaped or trilobed segments. Distalmost segments are cylindrical, 1.0–5.0 mm diam and 3.0–8.0 mm long. Utricles occur in 3–5 layers. Subsurface utricles are oval to clavate, 25–90  $\mu\text{m}$  diam and 23–100 long, each bearing 2–4 surface utricles. Peripheral utricles measure (23–)30–60(–74)  $\mu\text{m}$  diam in surface view and are 45–115  $\mu\text{m}$  long. Medullary siphons are fused in groups of 2, 3, or more. Algae are dark green in color.

**Habitat and Comments:** *Halimeda monile* typically occurs in shallow, protected sandy habitats and in seagrass beds in Puerto Rico. Littler and Littler (2000) reported the species in the Caribbean down to 30 m depths. A specimen (US Alg. Coll. 68658, M. Howe 7132) collected at Guayanilla Bay (25.VI.1915) fits the criteria for *Halimeda monile* f. *cylindrica* (Børgesen) Collins et Herv. (see Børgesen 1913: 113, fig. 91). The forma is considered to be synonymous with *H. monile*.

### ***Halimeda simulans* M. Howe**

FIGURE 56

*Halimeda simulans* M. Howe 1907: 503, pl. 29.

*Homotypic Synonym:* *Halimeda incrassata* var. *simulans* (M. Howe) Børgesen 1911: 144, fig. 11.

**Puerto Rican Records:** As *Halimeda simulans*: Howe 1915; Taylor 1960; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002.

**Western Atlantic Distribution:** Belize, Guadeloupe, Panama, North America, Bermuda, Bahamas, Cuba, Dominica, Grenadines, Hispaniola, Martinique, Netherlands Antilles, Puerto Rico, St. Barthélemy, Turks and Caicos Islands, U.S. Virgin Islands, Brazil, Colombia.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Isla Culebra, off east coast of Puerto Rico.

Thalli, to 15 cm tall, are freely branched in one plane, most commonly above a short cylindrical stipe that is either a single segment or, occasionally, 2–3 fused basal segments,

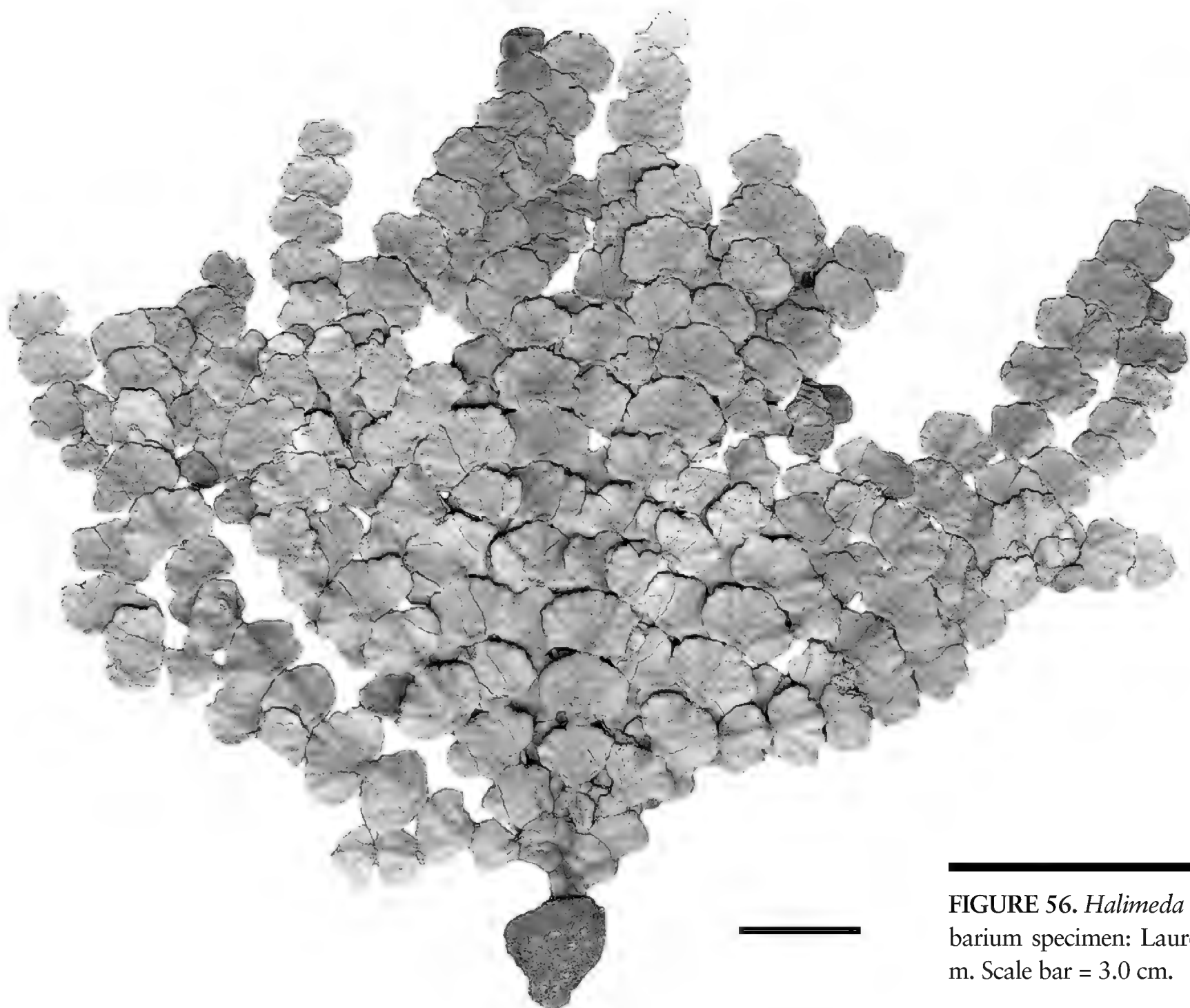


FIGURE 56. *Halimeda simulans*. DLB5342, herbarium specimen: Laurel Reef, La Parguera, 15 m. Scale bar = 3.0 cm.

up to 7.0 mm long and 4.0 mm diameter, that arise from a bulbous rhizoidal mass. The segments are well calcified and broadly oval to reniform, slightly ribbed, to 15 mm wide and 2.0–10 mm long. Segment lower margins are straight or concave; the upper margins are entire or somewhat trilobed. Utricles occur in 3–5 layers. Subsurface utricles are 30–70  $\mu\text{m}$  in diameter and 30–115  $\mu\text{m}$  long; each produces 2–4 surface utricles, 27–45(–60)  $\mu\text{m}$  in diameter and 25–90  $\mu\text{m}$  long. Medullary siphons are fused at joints between the segments. Algae are green in color.

*Habitat and Comments:* *Halimeda simulans* occurs in moderately shallow water, growing in sheltered sandy habitats, at mangroves fringes, and in seagrass beds, and, more rarely, in deeper water down to 73 m depths. Bearing a strong superficial resemblance to *H. incrassata*, the two can be easily confused in the field. *Halimeda simulans* has slightly ribbed segments and spherical surface utricles, whereas *H. incrassata* has strongly ribbed segments and angular surface utricles. [Additional illustrations: Taylor 1960: pl. 24: fig. 4; Braune and Guiry 2011: fig. 21.6.]

#### KEY TO THE *OSTREOBIUM* SPECIES OF PUERTO RICO

1. Filaments undifferentiated, either cylindrical or inflated, and uniform along their entire length with constrictions; chloroplasts spherical, small . . . . . *O. constrictum*  
 Filaments dimorphic, with both cylindrical and gradually inflated to swollen, intercalary to terminal saclike portions; chloroplasts reticulate and highly variable in size and shape . . . . . *O. quekettii*

#### *Ostreobium constrictum* Lukas

*Ostreobium constrictum* Lukas 1974: 334, figs. 6–8.

*Puerto Rican Records:* Ballantine and Norris 1989; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Belize, North America, Bermuda, Bahamas, Cuba, Jamaica, Netherlands Antilles, Puerto Rico, St. Lucia.

*Type Locality:* Discovery Bay, St. Ann Parish, north coast of Jamaica.

Thalli endolithic, filaments are cylindrical or inflated and constricted at intervals, possessing a sausage-like appearance, and 3.0–20  $\mu\text{m}$  in diameter, with inflated portions 13–60  $\mu\text{m}$  diam. Chloroplasts are spherical, 2.0–3.0  $\mu\text{m}$  diam.

*Habitat and Comments:* Algae are inconspicuous because of their endolithic habitat. In Puerto Rico, the species may be found within mollusk shells and coral skeletal fragments to a depth of 5.0 m in La Parguera. The species has been reported in Bermuda from 1.5 to 60 m depths (Lukas 1974) and in St Croix (U.S. Virgin Islands) from the intertidal to 15 to 30 m depths (Perkins and Tsentas 1976: fig. 46). The type specimen was endolithic within a colony of *Siderastrea siderea* (Anthozoa; Scleractinia), 8 m depth

#### OSTREOBINEAE VERBRUGGEN ET GUIRY

#### OSTREOBIACEAE P. C. SILVA EX MAGGS ET J. BRODIE

#### *Ostreobium* Bornet et Flahault

*Ostreobium* Bornet et Flahault 1889.

*Ostreobium* is an endolithic genus of microscopic, branched, coenocytic siphonaceous filaments living within calcareous substrata. These algae are generally inconspicuous and often overlooked because of their endolithic habitat. Thalli are ovoid or entirely cylindrical and irregularly to highly branched filaments, with or without inflated or swollen portions.

*Notes:* The genus *Ostreobium* currently contains at least five species separated by their morphological characteristics (e.g., Perkins and Tsentas 1976; Kornmann and Sahling 1980; May et al. 1982; Kobara and Chihara 1992). Lukas (1974) concluded that in the Atlantic and Caribbean there were three distinct species of *Ostreobium*. Two of those *Ostreobium* species have previously been reported for Puerto Rico.

(Lukas 1974). [Illustrations: Lukas 1974: figs. 6–9; Perkins and Tsentas 1976: figs. 25–27, 37–39.]

#### *Ostreobium quekettii* sensu Lukas

*Ostreobium quekettii* sensu Lukas 1974: 332, figs. 1–5 [non *Ostreobium quekettii* Bornet et Flahault 1889: 161, pl. 9, figs. 5–8.

*Puerto Rican Records:* Almodóvar and Blomquist 1965; Lukas 1974; Almodóvar et al. 1979; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Belize, North America, Bermuda, Bahamas, Jamaica, Netherlands Antilles, Puerto Rico (sensu Lukas 1974 only).

*Type Locality:* Le Croisic, Department Loire-Atlantique, western France.

*Ostreobium quekettii* is the generitype. Thalli are microscopic filaments within corals, shells, and coral skeletal fragments, 1.0–8.0  $\mu\text{m}$  diam (Puerto Rican specimens: 4.0–5.0  $\mu\text{m}$  diam), that are straight and sparsely branched or highly and repeatedly branched with many irregular branches that sometimes become entangled or knotted. Branches are irregular and taper to 2.0  $\mu\text{m}$  in diameter, with intercalary

or terminal swellings of 20–40 µm diam or with gradual inflated swelling. Branches occasionally possess thickened walls. Each order of branches successively decreases in diameter. Chloroplasts are reticulate and vary greatly in size and shape.

*Habitat and Comments:* For Puerto Rican specimens, identification follows the morphological characterization of *O. quekettii* sensu Lukas (1974). Puerto Rican *Ostreobium quekettii* occurs in the intertidal within mollusk shells and coral skeletal fragments and presumably extends into deep water. In the Bahamas specimens also referred to *O. quekettii* have been collected in deep water at greater than 200 m depths (Aponte and Ballantine 2001).

A broadly defined species, worldwide in distribution, “*O. quekettii*” is reported from the Arctic to the Antarctic in the Atlantic, Pacific, and Indian Oceans (Guiry and Guiry 2022). The taxonomy of *Ostreobium* in the western Atlantic needs further elucidation. Kornmann and Sahling (1980) were doubtful that material considered to be *O. quekettii* sensu Lukas (1974) was in accordance with the type species. Thus, Caribbean specimens are probably a different species. In fact, Sauvage et al. (2016) revealed that there were 85–95 genetically defined, but unnamed, cryptic endolithic species of boring endolithic microsiphons that belong in two different suborders of the Bryopsidales, raising the possibility that one of those unnamed entities may be the species that has been reported from Puerto Rico or that more than one species has been referred to *O. quekettii*. In a study of carbonate borers in the U.S. Virgin Islands, Perkins and Tsentas (1976) reported that one of the more common boring endolithic species (in neighboring U.S. Virgin Islands) was *Ostreobium brabantium* Weber Bosse 1932. The latter species possess substantially larger filaments than the Puerto Rican taxon. Perkins and Tsentas (1976) did not report the presence of *O. quekettii*. [Illustrations: Kylin 1949: fig. 66; Lukas 1974: figs. 1–5; Cormaci et al. 2014: FP273, fig. 4.]

**RHIPILIACEAE DRAGASTAN, D. K. RICHTER, KUBE, POPA, SARBU, ET CIUGULEA NOM. INVALID**

**RHIPILEAE HILLIS-COL.**

***Boodleopsis* A. Gepp et E. Gepp**

*Boodleopsis* A. Gepp et E. Gepp 1911.

Thalli are noncalcified and coenocytic, forming green cushions of loosely interwoven, highly irregularly or ditrichotomously branched filaments. Lower siphons are larger and thicker, attaching by rhizoids where in contact with substrata. The distal filaments are sharply constricted at their bases. Chloroplasts lack pyrenoids. Nine species of *Boodleopsis* are recognized, one of which is known from Puerto Rico.

*Note:* Cremen et al. (2019) found *Boodleopsis* to be polyphyletic, and *B. pusilla* was assigned to the Rhipileae.

***Boodleopsis pusilla* (Collins) W. R. Taylor, A. B. Joly, et Bernat.**

*Boodleopsis pusilla* (Collins) W. R. Taylor, A. B. Joly, et Bernat. 1953: 105, pls. 1–3.

*Basionym:* *Dichotomosiphon pusillus* Collins 1909a: 431.

*Puerto Rican Records:* As *Boodleopsis pusilla*: Taylor 1960; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Costa Rica, North America, Bermuda, Bahamas, Cuba, Guadeloupe, Jamaica, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, Brazil, Colombia, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* West Indies.

Thalli form matted turfs, composed of ditrichotomously or somewhat irregularly branched siphons. Siphons are mostly cylindrical to slightly moniliform, constricted at the base of each branch, and mostly without cross walls. The lower colorless siphons are buried in the substratum and measure to 90 µm diam. The upper filaments are more highly branched and measure 23–45 µm diam. Sporangial structures are pyriform to subspherical, measuring 60–153 µm diam and 83–207 µm long. Algae are bright green in color.

*Habitat and Comments:* *Boodleopsis pusilla* is often inconspicuous, forming clumps or turf-like mats on intertidal calcareous rocks and mud beneath mangroves near the high-tide line, and is associated with epiphytes on mangroves. [Illustrations: Calderon-Saenz and Schnetter 1989: figs. 16–18; Littler and Littler 2000: 395.]

***Rhipilia* Kütz.**

*Rhipilia* Kütz. 1858.

Thalli are uncalcified, with or without an ecorticate stipe bearing peltate, funnel-shaped, or fan-shaped foliar fronds. Blades are composed of a multilayered meshwork of interwoven dichotomous to irregularly branched siphons. Siphons may be constricted in the vicinity of branching and terminate in 2–6 blunt to spinelike tentacular appendages that attach tips to adjacent siphons of blades. Twelve species of *Rhipilia* are recognized worldwide, including a single species from Puerto Rico.

*Note:* *Rhipilia* superficially resembles *Avrainvillea* but differs by its tentacular attachments and complete lack of differentiation into a distinct cortex and medulla.



***Rhipilia tomentosa* Kütz.**

FIGURE 57

*Rhipilia tomentosa* Kütz. 1858: 12, pl. 28: fig. I.

*Puerto Rican Records:* Howe 1915; Taylor 1960, Almodóvar and Ballantine 1983; Millar and Kraft 2001; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* North America, Bahamas, Antigua, Cuba, Guadeloupe, Puerto Rico, U.S. Virgin Islands, Brazil.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Antigua Island (Antigua and Barbuda), Leeward Islands, eastern Caribbean.

*Rhipilia tomentosa* is the generitype species. Stipes are attached to the substrata by prostrate stolon-like axes and/or

rhizoidal tufts; they are 5.0–10 mm long and 3.0–5.0 mm diam or in some cases are lacking. Stipe siphons measure to 50  $\mu$ m diam. Each stipe bears a cuneate, rounded, peltate, or funnel-shaped flabellum that may be thin to moderately thick and spongy, 3.0–4 cm wide, to 4.0 cm long. Structural siphons of the blade are 30–70  $\mu$ m diam. They are thin walled, loosely interwoven, and branched pseudodichotomously, being constricted equally at the dichotomous forks and unequally at nondichotomous branching sites. The siphon tips are slightly clavate, bearing clavate siphons, 33–60  $\mu$ m in diameter and 50–200  $\mu$ m long, that terminate with tentacular projections and attach to adjacent siphons.

*Habitat and Comments:* Once considered a species of moderate depths, in Puerto Rico *Rhipilia tomentosa* occurs on sand plains to 30 m depths, as well as in shallow-water habitats, in tide pools, and on exposed reefs. Taylor (1960) also reported that the species has been dredged to depths of 73 m. [Additional illustrations: Gepp and Gepp 1911: pl. 15, figs. 126–128.]



FIGURE 57. *Rhipilia tomentosa*. In situ habit photograph from Bahia Sucia, Cabo Rojo, 1.0 m, growing among *Amphiroa fragilissima* (L.) J. V. Lamour. Field = approximately 30 cm.



**RHIPILIOPSIDAE CREMEN, LELIAERT, J. A. WEST,  
D. W. LAM, ET VERBRUGGEN**

On the basis of their molecular sequencing, Cremen et al. (2019) proposed integration of the Rhipiliopsidae into a more broadly circumscribed Halimedaceae.

**Rhipiliopsis A. Gepp et E. Gepp**

*Rhipiliopsis* A. Gepp et E. Gepp 1911.

**KEY TO THE RHIPILIOPSIS SPECIES OF PUERTO RICO**

1. Thalli in aggregations, stipe near blade multisiphonous, lower portion a single siphon; blades netlike, flat, fan shaped, often lobed or proliferous ..... *R. stri*  
Thalli solitary; stipe of several siphons above from a single siphon at the holdfast; blades netlike, funnel shaped when young, becoming peltate to fan shaped ..... *R. reticulata*

**Rhipiliopsis reticulata (C. Hoek) Farghaly et Denizot**

*Rhipiliopsis reticulata* (C. Hoek) Farghaly et Denizot 1979: 181.

*Basionym*: *Udotea reticulata* C. Hoek 1978: 57, figs. 8, 9.

*Puerto Rican Records*: As *Rhipiliopsis reticulata*: Ballantine and Aponte 2002; Ballantine et al. 2016.

*Western Atlantic Distribution*: Panama, Bahamas, Cuba, Netherlands Antilles, Puerto Rico, Colombia.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Klein Piscadera, Curaçao, Netherlands Antilles.

Thalli are noncalcified and 2.0–8.0 mm tall. The stipes are short, measuring 250–500 µm long and 65–100 µm diam above a holdfast of short rhizoids. Stipes are originally a single siphon that branches trichotomously above where it expands into the terminal flabellum. The blades are initially fan shaped, becoming flat, and composed of siphons in a single layer, these measuring 35–65 µm diam. Adjoining siphons are laterally attached periodically by short branchlets resulting in open gaps, giving the blade a reticulate or netlike appearance.

*Habitat and Comments*: In Puerto Rico *Rhipiliopsis reticulata* is inconspicuous but not uncommon on rubble in deepwater, coral reef environments, 49–82 m depths (Ballantine et al. 2016). Described from deep water, 20–60 m (Hoek 1978, as *Udotea reticulata*), it is reported in the Bahamas from 92 m (Norris and Olsen 1991) and from Cuba in shallow-water, low-light habitats, 5–15 m depths (Guimaraes Bermejo et al. 2014; Suarez et al. 2015). It is probably of wider occurrence in the Caribbean than indicated by the currently known distribution. [Illustration: Littler and Littler 2000: 415.]

Noncalcified thalli reach 5.0 mm or less to more than 7.0 cm tall. Monosiphonous or polysiphonous stipes arise from a prostrate rhizome and bear flabella consisting of irregularly lanceolate or peltate (sometimes off-center) flabella. Blades possess dichotomously branched siphons that are generally equally constricted above dichotomies. In the two species with thickest blades, a somewhat differentiated cortex develops on upper and lower surfaces of fronds. Flabellar siphons cohere at scattered and isolated points by circular rings of wall thickening at tips of lateral papillae or truncated blade-siphon dichotomies. Scattered spines occur on blade siphons of two species. Two *Rhipiliopsis* species are known from Puerto Rico, and 17 species are known worldwide.

**Rhipiliopsis stri (S. A. Earle et J. R. Young)  
Farghaly et Denizot**

FIGURE 58

*Rhipiliopsis stri* (S. A. Earle et J. R. Young) Farghaly et Denizot 1979: 182.

*Basionym*: *Siphonoclathrus stri* S. A. Earle et J. R. Young 1972: 3, figs. 1–8.

*Puerto Rican Records*: As *Rhipiliopsis stri*: Ballantine and Wynne 1986; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution*: Costa Rica, Mexico, Panama, Netherlands Antilles, Puerto Rico, Brazil, Colombia.

*Type Locality*: On limestone in 8 m depth, Galeta Reef, Caribbean Sea, Panama [vicinity of Smithsonian Tropical Research Institute (STRI) Galeta Marine Lab, Punta Galeta, Colón, Caribbean Panama].

Thalli are gregarious and reach to 20 mm high, attached by a base of entangled rhizoids. Stipes are often branched and consist of several intertwined siphons, to 40 µm diam. Blades are fan shaped and flattened, netlike, often lobed or proliferating, to 5.0 mm long. Blade siphons are cylindrical, averaging 40 µm diam, and occur in 1 layer. The siphons are parallel and adherent laterally by short connecting lateral branchlets. The siphons are constricted above di- and trichotomies.

*Habitat and Comments*: Restricted to the western Atlantic, *Rhipiliopsis stri* occurs at 49–70 m depths in Puerto Rico (Ballantine et al. 2016). Although often found in deep water, it was described from shallow waters of Caribbean Panama, 5–10 m depths (Earle and Young 1972) and reported on limestone, coral rubble, and shells from the intertidal to 11 m depths (Littler and Littler 2000). Bula-Meyer (1982) and Silva et al. (1996) treated *R. stri* and *R. reticulata* as conspecific. This opinion was



FIGURE 58. *Rhipiliopsis stri*. DLB1808: Edge of insular shelf, La Parguera, 50 m. Portion of flabellum. Scale bar = 500  $\mu$ m.

followed by Ballantine and Wynne (1986) in reporting *R. stri* from Puerto Rico. Nevertheless, Wynne (2017) and Guiry and Guiry (2022) currently treat the two species as being independent. [Additional illustrations: Littler and Littler 2000: 141; Mateo Cid et al. 2002: figs. 26–28.]

#### UDOTEAE KONISHI

#### *Johnson-sea-linkia* Eiseman et S. A. Earle

*Johnson-sea-linkia* Eiseman et S. A. Earle 1983.

Thalli possess an erect stipe, usually with a single terminal peltate blade, attached below by a rhizoidal holdfast. The stipe occasionally divides, and additional perfoliate blades may be present. Stipes are composed of intertwined, interconnected siphons that produce a blade composed of a single layer of laterally adherent filaments and sparse superficial filaments that

crisscross the blade. Growth occurs at the blade margin. Siphons contain numerous, discoid chloroplasts, each with a single indistinct pyrenoid, and lack leucoplasts.

*Note:* Although treated as a synonym of *Rhipiliopsis* (Norris and Olsen 1991), recent phylogenomic analyses of *Johnson-sea-linkia profunda* found that it differed molecularly from the generitype of *Rhipiliopsis*, and the genus was reinstated (Cremen et al. 2019).

#### *Johnson-sea-linkia profunda* Eiseman et S. A. Earle

FIGURE 59

*Johnson-sea-linkia profunda* Eiseman et S. A. Earle 1983: 1, figs. 3–9.

*Heterotypic Synonym:* *Rhipiliopsis profunda* (Eiseman et S. A. Earle) J. N. Norris et Blair in J. Norris and Olsen 1991: 324.

*Puerto Rican Records:* As *Rhipiliopsis profunda*: Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution:* Mexico, Bahamas, Cayman Islands, Puerto Rico.

*Type Locality:* Grand Bahama Island, Bahamas.

Peltate thalli are to 6.0 cm tall. The stipes measure 2.0–6.0 mm long and 0.3–0.5 mm diam and are attached by a very small rhizoidal holdfast. Stipes are mostly simple or only occasionally branched and composed of a central core of siphons, each 14–16  $\mu$ m diam; outer stipe siphons with short, slender lateral branches that are entwined to form a cortex. Foliar portions or blades are peltate and circular, to 3.5 cm. diam and 20  $\mu$ m thick. Blades are unistratose, composed of laterally adherent parallel filaments, 12–16  $\mu$ m diam with seeming randomly placed cross filaments. The cross filaments are solely on the dorsal surface. Algae are light, translucent green in color.

*Habitat and Comments:* The species is rarely collected in Puerto Rico, being an exclusively deepwater species. *Johnson-sea-linkia profunda* has been dredged to 70 m at Mona Island. Puerto Rican plants possess stipes 2.0–6.0 mm long supporting cyathiform blades that measure to 25 mm across. Blades of Puerto Rican specimens are composed of filaments measuring 12–20  $\mu$ m diam. Puerto Rican plants are thus somewhat smaller than Bahamian plants that measure to a height of 7 cm with a blade width of 34 mm. Possibly the deepest erect, noncalcified green alga known, *J. profunda* occurs in the Bahamas from 61 to 131 m depths (Norris and Olsen 1991) and down to 153 m off Freeport, Grand Bahama Island. Almost exclusively a deep-water species, *J. profunda* reportedly also occurs in shallower,



FIGURE 59. *Johnson-sea-linkia profunda*. DLB3607: South Mona Island, 60 m. Scale bar = 1.0 cm.

low-light habitats of caves and undercut ledges of Cozumel island, Mexico, to a minimum of 11 m depth (Littler and Littler 2000).

*Notes:* Members of what have been referred to the Udoteaceae have received a great deal of recent attention, largely because of the recognition of polyphyly in many of its genera on the basis of multiple genetic markers (Curtis et al. 2008; Verbruggen et al. 2009; Lagourgue et al. 2018). On the basis of their molecular sequencing, Cremen et al. (2019) proposed integration of the

Udoteaceae into a more broadly circumscribed Halimedaceae. Despite superficial morphological expressions that have helped define individual genera, some members (*Penicillus* for one) do not appear to be genetically similar. Lagourgue and Payri (2020) recognized two large species complexes, one including *Penicillus*, *Rhipidosiphon*, *Rhipocephalus*, and *Udotea* and the other including *Poropsis*, *Penicillus*, and *Rhipidodesmis*. They estimated the origin of the family at about 216 MA.

### ***Penicillus* Lam.**

*Penicillus* Lam. 1813.

Stalked thalli are erect, calcified, and arise from an anchor of tangled rhizoids and adherent sand. The simple stalks terminate in a capitular tuft of dichotomously branching filaments. Capitular filaments are bright green at the growing tips, becoming whitened by calcification as they mature; growth of the capitulum filaments is determinate, with little or no further development once it matures. Capitular siphons are dichotomously or occasionally trichotomously branched in more than one plane. Filaments of the stalk are oriented longitudinally and radially branched, forming a core of medullary siphons and a simple cortex. Siphon walls are noncellulose, composed mostly of  $\beta$ -1,3-xylan. Both chloroplasts, either with or without starch, and amyloplasts are present.

*Notes:* Once considered a separate genus, *Espera* Decne. (1842a) was discovered to be the juvenile form or “*Espera* state” of *Penicillus* (see Friedmann and Roth 1977). Although Gepp and Gepp (1911) suggested two distinct forms of development in *Penicillus*, Meinesz (1972, 1980) later showed that there was only one developmental pattern, in which the developing stipe gives rise to a capitulum. Phylogenetic analysis has revealed that the *Penicillus* morphology has independently arisen twice (Kooista 2002: 453), and a critical phylogenetic and systematic revision of the genus is needed. Four of the nine currently recognized species of *Penicillus* occur in Puerto Rico.

### KEY TO THE *PENICILLUS* SPECIES OF PUERTO RICO

1. Capitulum filaments branching at wide angles, tangled ..... *P. pyriformis*  
    Capitulum filaments branching at narrow angles, generally lying nearly parallel ..... 2
2. Capitular filaments 125–200  $\mu$ m diam, 2.0–3.0 cm long ..... *P. capitatus*  
    Capitular filaments greater than 300  $\mu$ m diam, generally longer than 3.0 cm ..... 3
3. Plants heavily calcified; capitular filaments 300–500  $\mu$ m diam ..... *P. lamourouxii*  
    Plants lightly calcified; capitular filaments 400–800  $\mu$ m diam ..... *P. dumetosus*

***Penicillus capitatus* Lam.**

FIGURE 60

*Penicillus capitatus* Lam. 1813: 299 (lectotype species of the genus).

*Heterotypic Synonym:* *Corallina penicillus* L. 1758: 807.

*Puerto Rican Records:* As *Penicillus capitatus*: Almodóvar and Blomquist 1959, 1961; Taylor 1960; Almodóvar 1964a, 1964b; Almodóvar and Pagán 1971; Schwartz and Almodóvar 1971; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution:* Belize, Costa Rica, Mexico, Panama, North America, Bermuda, Bahamas, Antigua, Cayman Islands, Cuba, Dominica, Grenadines, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, Barthélemy, St. Eustatius, St. Kitts, St. Martin, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Netherlands Antilles, Brazil, Colombia, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* “Les mers d’Amérique” (Lamarck 1813: 299). Note that Linnaeus (1758: 807) gave “habitat in Asia” for *Corallina penicillus*; however, this is unlikely in that *P. capitatus* is unknown from Asia in the Indian or Pacific Oceans (Spencer et al. 2009) and occurs only in the western Atlantic from Bermuda to Brazil, the Mediterranean, and Madeira. Leliaert (in Spencer et al. 2009: 246) selected a lectotype of *Corallina penicillus* L., noting that its identity could not be confirmed (destructive sampling prohibited by the Herbarium Linneaus) and that an epitype may need to be selected.

*Penicillus capitatus* is the generitype species. Thalli are 2.0–25 cm tall and are composed of a brush-like capitulum occurring terminally on a stipe. The stipes, 3.0–10 cm long and to 3.0 mm diam below and to 7.0 mm diam above, are attached by a rhizoidal mass and sand anchor. The stipe somewhat penetrates into the capitulum. Cortical stipe filaments possess closely branched lateral projections that are truncate and thickened at the slightly capitate tips. The capitula are oblate-spherical to somewhat pyriform, measuring 2.0–6.0 cm long and 2.0–6.0 cm wide. The capitula are composed of dichotomously branched, slightly calcified filaments. Capitular filaments are compact, mostly 2.0–3.0 cm long, and 73–300 µm diam. Algae are dull gray green in color.

*Habitat and Comments:* In Puerto Rico, *Penicillus capitatus* is extremely common in shallow-water seagrass and reef flat habitats, as well as in moderate-depth algal plain habitats, and is more rarely found in deeper water, 80–100 m depths (Ballantine et al. 2016). The phylogenetic tree presented by Kooistra (2002: fig. 2) shows *P. capitatus* in a clade with *Udotea abbottiorum* D. S. Littler et Littler and *U. cyathiformis* Decne., an indication that a broad taxonomic revision is needed. [Additional illustrations: Gepp and Gepp 1911: pl. 20, figs. 167b, 168; Harvey 1858: pl.



FIGURE 60. *Penicillus capitatus*. DLB1-56, herbarium specimen: Seaward Media Luna Reef, La Parguera, 17 m. Scale bar = 1.0 cm.



43B; Taylor 1960: pl. 21: fig. 2, pl. 25: fig. 4; Friedmann and Roth 1977: figs. 1A–E, 2F,H, 3A–C, F, 4D,F, pls. 2B,E,F,H,I, 3A,C, 4B,D,E, 5A–C; Littler et al. 2008: 228.]

***Penicillus dumetosus* (J. V. Lamour.) Blainv.**

FIGURE 61

*Penicillus dumetosus* (J. V. Lamour.) Blainv. 1830: 516.

*Basionym*: *Nesaea dumentosa* J. V. Lamour. 1816: 259, pl. 8: figs. 3a, 3.

*Puerto Rican Records*: Taylor 1960; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution*: Belize, Mexico, Panama, North America, Bermuda, Bahamas, Anguilla, Antigua, Cuba, Cayman Islands, Grenadines, Guadeloupe, Hispaniola, Jamaica, Martinique, Puerto Rico, St. Barthélemy, St. Kitts, U.S. Virgin Islands, Colombia, Venezuela, Caribbean.

*Type Locality*: “Mer des Antilles.”

Thalli reach 30 cm tall and are lightly calcified. Plants are attached by a rhizoidal mass and sand anchor. Singular stipes, sometimes branched, measure 2.0–8.0 cm long and 15–25 mm diam. The stipes are often compressed above and taper slightly into the capitula. Cortical filaments of the stipe are loosely, dichotomously branched, tapering terminally to blunt, thick-walled apices. Capitula are soft, rounded, and obovoid, to 10–15 cm long and longer than wide. The loosely arranged capitular filaments are lightly calcified proximally, measuring 3.5–8.0 cm long and 400–800 µm diam. Algae are gray green in color.

*Habitat and Comments*: *Penicillus dumetosus* is found in shallow waters to 15 m depths in protected sandy environments, such as seagrass beds. The phylogenetic analysis of Kooistra (2002: fig. 2) indicated that *P. dumetosus* is in a separate clade from the type species, *P. capitatus*, providing further evidence that the systematics and relationships within the genus require further study. [Additional illustrations: Harvey 1858: pl. 43A; Gepp and Gepp 1911: pl. 18: figs. 157–158, pl. 19: figs. 156–159; Taylor 1960: pl. 21: fig. 4, pl. 25: fig. 15; Friedmann and Roth 1977: fig. 2I, pls. 1, 2G, 3B,D; Braune and Guiry 2011: fig. 22.2.]

***Penicillus lamourouxii* Decne.**

FIGURE 62

*Penicillus lamourouxii* Decne. 1842a: 97, 109.

*Puerto Rican Records*: Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar 1964b; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution*: Belize, Panama, Mexico, North America, Bahamas, Cuba, Cayman Islands, Guadeloupe, Jamaica, Martinique, Puerto Rico, St. Eustatius, U.S. Virgin Islands, Turks and Caicos, Venezuela.

*Type Locality*: Bahamas.



FIGURE 61. *Penicillus dumetosus*. DLBsn, herbarium specimen: Vieques Island. Scale bar = 2.0 cm.

Conspicuously calcified thalli measure to 7.0 cm tall. Algae are attached by a rhizoidal mass and sand anchor. Stipes, 1.0–4.0 cm long and 5.0–8.0 mm diam, are often hollow and compressed, not penetrating into the capitulum. Stipe cortical filaments are abruptly inflated above the basal constriction, where they are closely branched with digitate tips. The rather loose capitula, to 5.0 cm long and 2.0–4.0(–5.0) cm diam, are oval to spherical. Filaments of the capitulum measure 300–500 µm diam. Algae are light green in color.

*Habitat and Comments*: *Penicillus lamourouxii* most commonly occurs in shallow protected sandy or muddy habitats, usually in seagrass beds, and in moderate depths to 12 m and has been dredged to 73 m (Taylor 1960). [Additional illustrations: Gepp and Gepp 1911: pl. 19, figs. 160–167; Taylor 1960: pl. 21: fig. 1, pl. 25: fig. 2; Friedmann and Roth 1977: figs. 3D,G, 4B,C,E, pls. 2A,C,D, 4C.]



FIGURE 62. *Penicillus lamourouxii*. SAEsn, herbarium specimen: Lameshur Bay, St. John, U.S. Virgin Islands. Scale bar = 1.0 cm.

### *Penicillus pyriformis* A. Gepp et E. Gepp

FIGURE 63

*Penicillus pyriformis* A. Gepp et E. Gepp 1905: 1, pl. 468: fig. 1a,b.

*Puerto Rican Records:* Taylor 1960; Almodóvar and Blomquist 1965; Ballantine 1977; Almodóvar et al. 1979; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Panama, Mexico, North America, Bermuda, Bahamas, Anguilla, Cuba, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, St. Eustatius, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

*Syntype Localities:* Bimini ("Bemini") Harbor, South Bimini, Bimini Islands, Bahamas; Eli's Harbor, Sommerset, Bermuda; and Key West, Florida Keys, Florida, USA (Gepp and Gepp 1905).

Erect thalli, measuring to 12 cm tall, are heavily calcified and attached by a rhizoidal mass and sand anchor. Stipes are spongy, terete or compressed above, measuring 3.0–10 cm long and 5.0–7.0 mm diam. The stipes barely penetrate the capitula and are superficially calcified. Corticating filaments of the stipe are loosely branched, terminally tapering to blunt, thickened apices. The capitula are cone shaped and flat topped, 3.0–7.0 mm long and 3.0–4.5 cm diam. Capitulum filaments are much entangled, measuring 2.0–3.0 cm long and 150–250  $\mu$ m diam. These filaments are forked at broad angles. Algae are gray green in color.

*Habitat and Comments:* *Penicillus pyriformis* occurs in shallow, protected sandy areas. Kooistra (2002: fig. 2) indicated that *P. pyriformis* is situated in a separate phylogenetic clade from the type species, *P. capitatus*. [Additional illustrations: Gepp and Gepp 1911: pl. 20, figs. 169–171; Børgesen 1913: fig. 81; Taylor 1960: pl. 21: figs. 3, 5, pl. 25: fig. 1; Friedmann and Roth 1977: figs. 3D,G, 4A, pl. 4A.]

### *Rhipidosiphon* Mont.

*Rhipidosiphon* Mont. 1842a: 14.

Thalli are small, possessing a holdfast composed of fine rhizoids. Thalli possess erect, partially calcified, monosiphonous stipes that lack cortication. The stipes bear fan-shaped, unistratose, calcified terminal flabella. The flabella possess dichotomously branched siphons that are constricted at the dichotomies. The siphons lie parallel in calcified sheaths and may be fused. There are three recognized *Rhipidosiphon* species, one of which is known from Puerto Rico.

*Note:* *Rhipidosiphon* differs from *Udotea* primarily by its characteristic monosiphonous, partially calcified stipe.

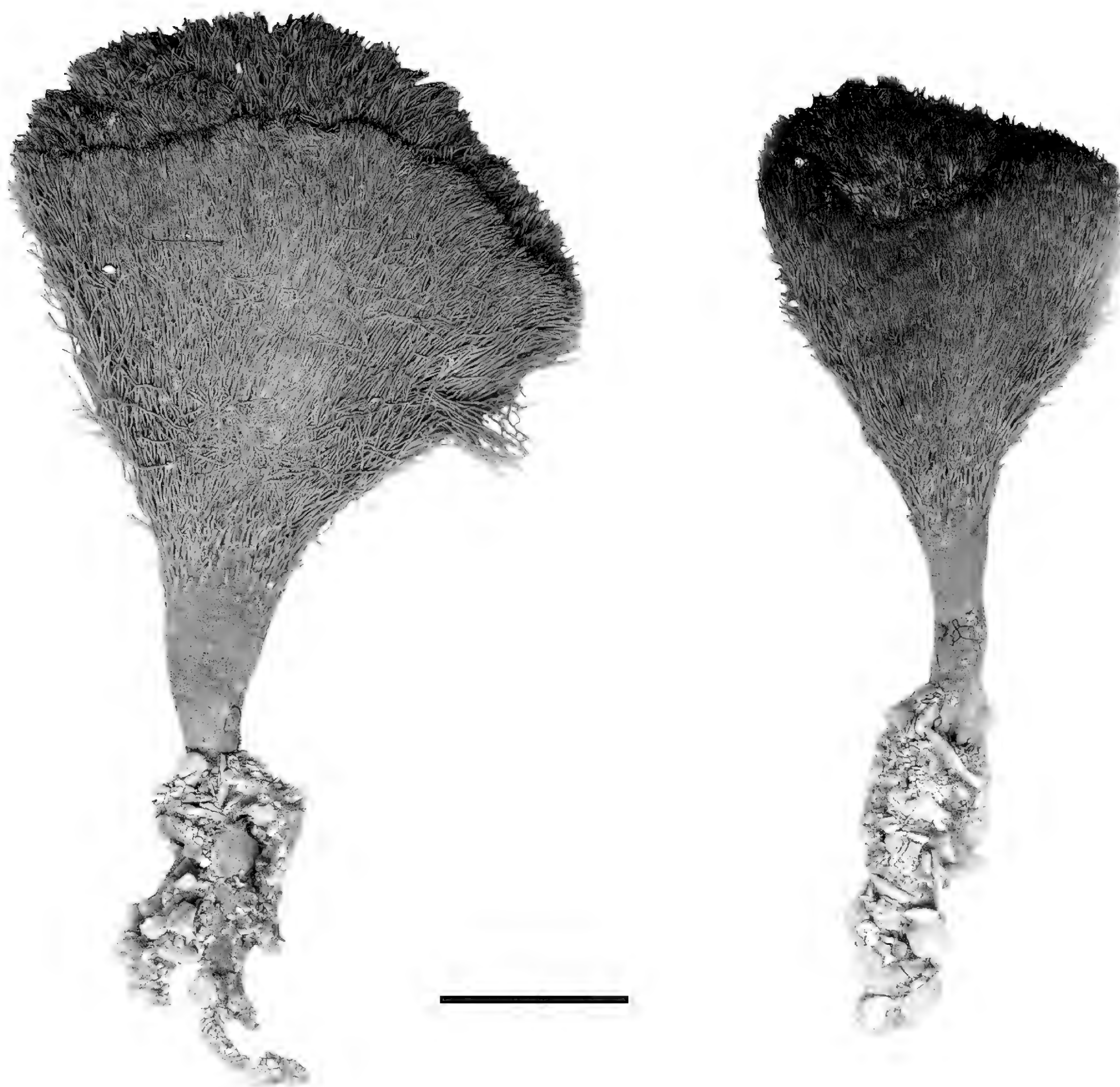


FIGURE 63. *Penicillus pyriformis*. DLBsn, herbarium specimen: Punta Arenas, Vieques. Scale bar = 1.0 cm.

***Rhipidosiphon floridensis* D. S. Littler et Littler**

FIGURE 64

*Rhipidosiphon floridensis* D. S. Littler et Littler 1990a: 34, figs. 1–5.

*Puerto Rico Records:* Littler and Littler 1990a; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Panama, North America, Puerto Rico.

*Type Locality:* Northwest of Loggerhead Key, Dry Tortugas, Monroe County, Florida, USA.

Erect thalli, reaching 10 mm tall, are attached to the substratum by fine rhizoids. The simple partially calcified stipe, 130–220 µm diam, is 1.0 mm long and bears a calcified monostromatic, uncorticated fan-shaped flabellum. The flabella are 8.0 mm long and 6.0 mm wide and are cuneate at the base, with rounded margins, frequently lacerate or torn. Blade siphons lie parallel and adhere laterally. The siphons are dichotomously divided with equal constrictions above the dichotomies. Siphons measure 95–116 µm diam proximally, decreasing to 45–60 µm distally.

*Habitat and Comments:* Algae are inconspicuous on hard substrata, to 20 m depth. One of the Puerto Rican plants collected and identified by D. S. Littler from the algal plain offshore from Media Luna Reef measures to 21 mm, greater than twice the height reported by Littler and Littler (1990a). Lagourgue and Payri (2020), on the basis of their broad systematic survey of the Udoteaceae, proposed to exclude *Rhipidosiphon floridensis* from *Rhipidosiphon*; however, they did not suggest a replacement genus. [Additional illustrations: Littler and Littler 1990a: figs. 1–5, 2000: 421; Mateo-Cid et al. 2002: figs. 23–25.]

***Rhipocephalus* Kütz.**

*Rhipocephalus* Kütz. 1843: 311.

Erect thalli are generally lightly calcified and anchored by a loose basal mass of rhizoids with adherent sand. Simple stalks produce a capitulum of either free (not fused) branched siphons or of laterally adherent siphons that form small blades. The blades are monostromatic, composed of branched filaments that are constricted above the dichotomies.

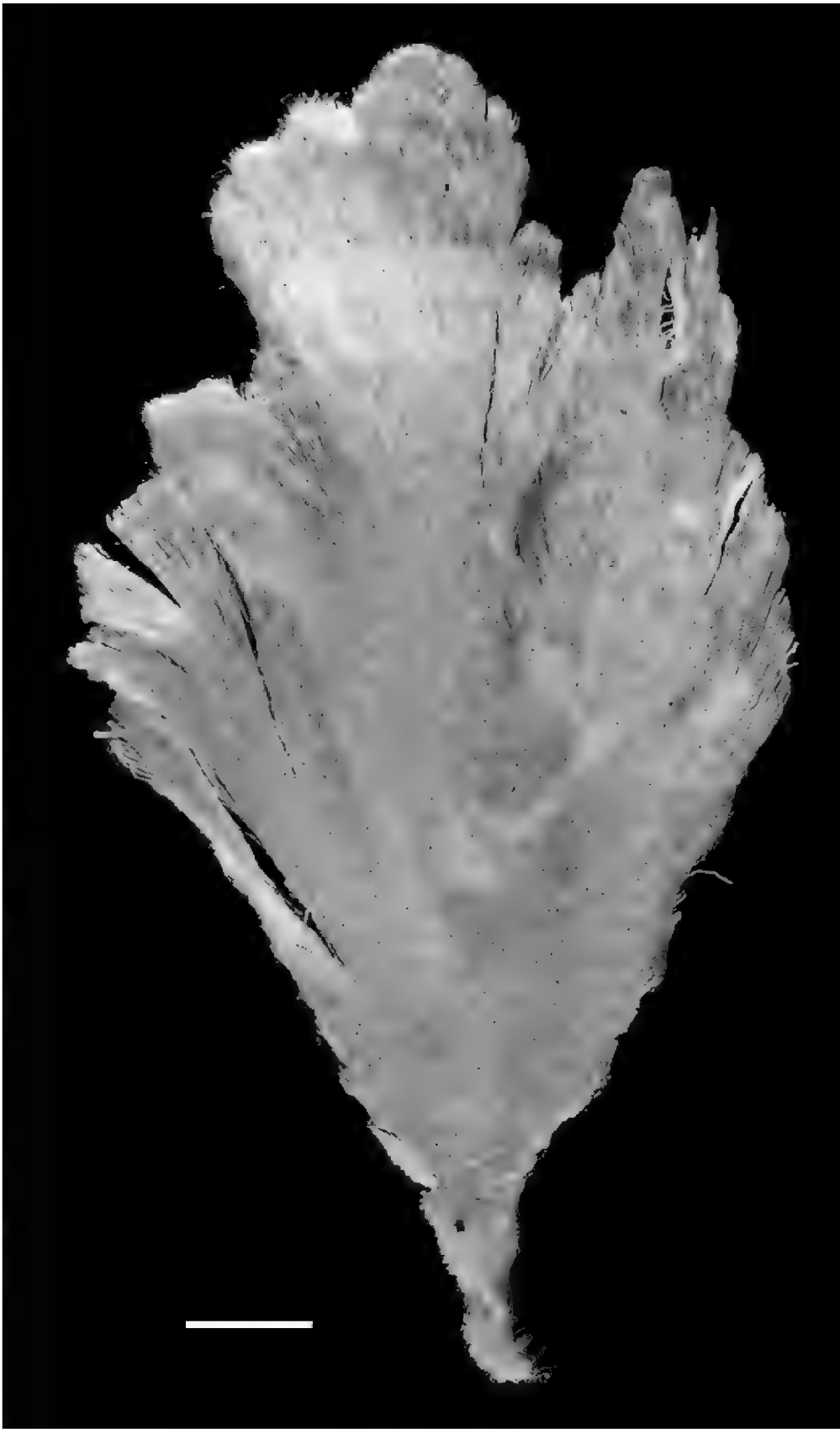


FIGURE 64. *Rhipidosiphon floridensis*. D&ML17320, herbarium specimen: Algal plain, seaward Media Luna Reef, 17 m. Scale bar = 2.0 mm.

*Notes:* Kooistra (2002) indicated that despite distinct morphological differences in appearance, *Udotea*, *Penicillus*, and *Rhipocephalus* are not well differentiated molecularly from each other. Both of the two recognized species of *Rhipocephalus* as well as one infraspecific taxa are known from Puerto Rico.

KEY TO THE *RHIPOCEPHALUS* SPECIES OF PUERTO RICO

- Capitulum filaments laterally fused to form small blades ..... *R. phoenix*  
Capitulum filaments when young may be laterally associated but do not form cohesive blades ..... *R. oblongus*



***Rhipocephalus oblongus* (Decne.) Kütz.**

FIGURE 65

*Rhipocephalus oblongus* (Decne.) Kütz. 1849: 506.

*Basionym*: *Penicillus oblongus* Decne. 1842a: 109.

*Puerto Rican Records*: As *Rhipocephalus oblongus*: Ballantine et al. 2015, 2016.

*Western Atlantic Distribution*: Mexico, North America, Bahamas, Cuba, Martinique Puerto Rico.

*Type Locality*: “Hab. in Antilles (Bahama).”

Thalli reaching 13 cm tall are composed of a cone-shaped or elongate capitulum, 5.0–15 cm long and 1.0–3.0 cm diam above a subterete or terete stipe, 4.0–7.5 cm long and to 6.0 mm diam, anchored below by a rhizoidal mass. The stipes continue into the capitula for 0.75 of their lengths. Cortical siphons of the



FIGURE 65. *Rhipocephalus oblongus*. DLB8469, herbarium specimen: Carabinero, Mona Island, 35 m. Scale bar = 1.0 cm.

stipe bear lateral appendages that terminate in blunt digitate tips. Capitulum siphons measure 200–350  $\mu$ m diam proximally and 160–200  $\mu$ m diam distally. When young, the capitulum siphons are associated laterally but not firmly cemented into small blades and become laterally independent with maturity. Algae are dark green to whitish.

*Habitat and Comments*: *Rhipocephalus oblongus* is typically found in shallow-water seagrass beds on sand or muddy bottoms and occurs to 36 m depths in Puerto Rico (Ballantine et al. 2015, 2016) and to 40 m in the Florida Keys. Puerto Rican specimens of *R. oblongus* are up to 7.0 cm in height, including the 2.0 cm long stipes that average 2.0 mm diam. The capitula bear few laterally joined siphons. The capitular siphons of Puerto Rican *R. oblongus* are up to 110  $\mu$ m in diameter and taper to 80  $\mu$ m distally, which are less than the filament dimensions (160–200  $\mu$ m) reported by Taylor (1960) for other Caribbean specimens. As the species is normally found in shallow-water habitats (Taylor 1960), the smaller siphon dimensions, observed in the deeper-water (36 m) Puerto Rican *R. oblongus* may be related to depth. [Additional illustrations: Gepp and Gepp 1911: pl. 21, fig. 189; Taylor 1960: pl. 22: fig. 1.]

***Rhipocephalus phoenix* (J. Ellis et Sol.) Kütz.**

FIGURE 66A

*Rhipocephalus phoenix* (J. Ellis et Sol.) Kütz. 1843: 311.

*Basionym*: *Corallina phoenix* J. Ellis et Sol. 1786: 126, pl. 25: figs. 2–3.

*Homotypic Synonym*: *Penicillus phoenix* (J. Ellis et Sol.) Lam. 1813: 299.

*Puerto Rican Records*: As *Rhipocephalus phoenix*: Taylor 1960; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution*: Mexico, Panama, North America, Bahamas, Antigua, Belize, Cuba, Guadeloupe, Hispaniola, Jamaica, Puerto Rico, Colombia.

*Type Locality*: Bahama Islands. The type apparently does not exist; the illustration of Ellis and Solander (1786: pl. 25: fig. 2) was selected as a lectotype by Gepp and Gepp (1905: 4).

*Rhipocephalus phoenix* is the generitype. Thalli, anchored by rhizoidal masses, are 7.0–12 cm tall with stipes measuring 2.0–10 cm long and 3.0–8.0 mm diam. Corticating stipe filaments are abundantly present, bearing digitate projections with blunt apices. The oval to cone-shaped capitula are composed of compact monostromatic, flattened blades, 2.0–5.0 cm long, concentric, and separate or torn. Blades are composed of parallel, laterally fused capitular siphons, 200–250  $\mu$ m diam proximally and 50–100  $\mu$ m diam distally. Algae are dull green in color.

*Habitat and Comments*: Although not common in Puerto Rico, *Rhipocephalus phoenix* occurs in shallow water, to 10 m depths, growing in sandy areas and seagrass beds and mangroves. In deeper sandy habitats of Puerto Rico, it has been collected down to 50 m depths (Ballantine et al. 2016), and elsewhere

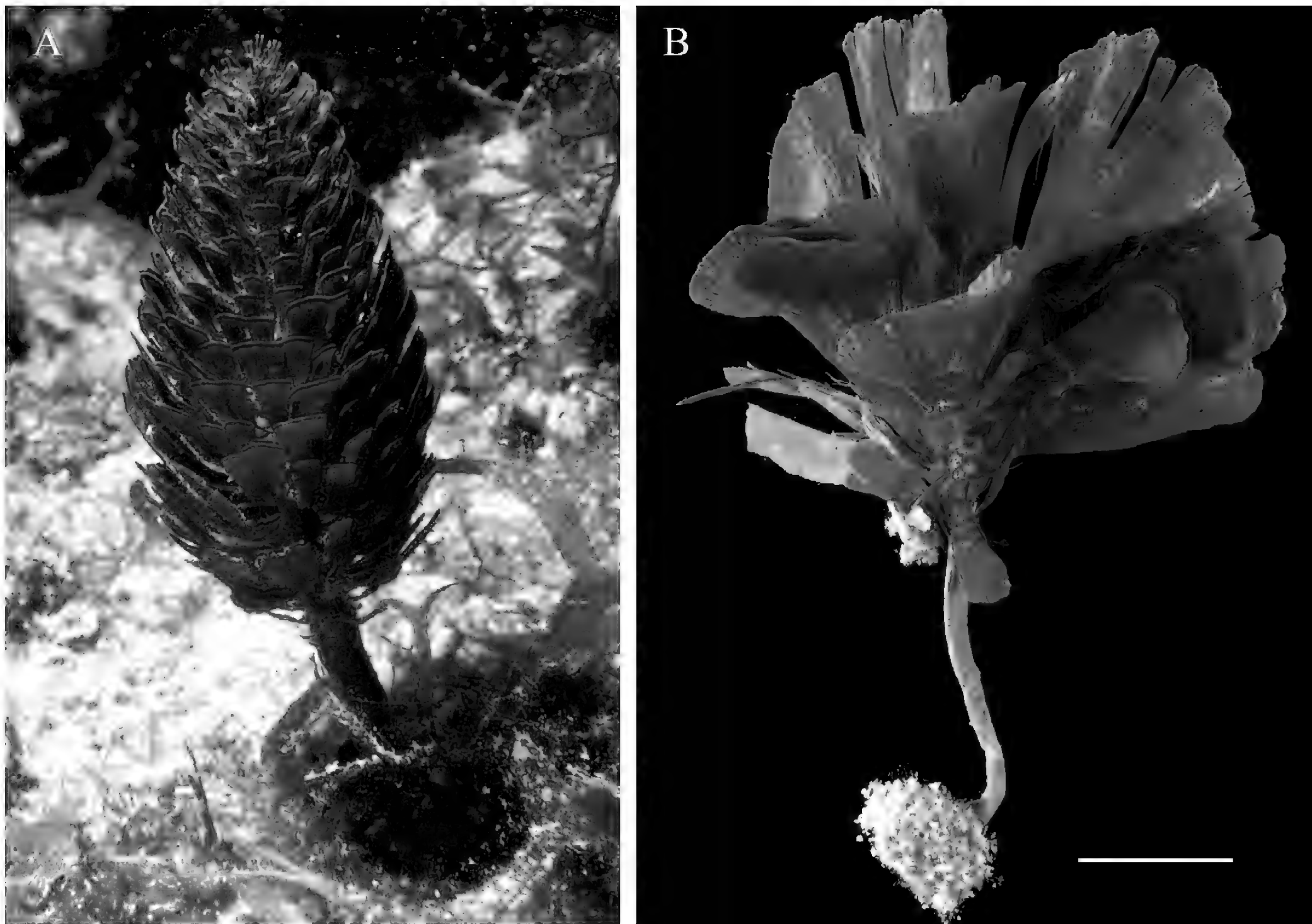


FIGURE 66. *Rhipocephalus phoenix*. (A) In situ habit photograph. Field = approximately 5.0 cm. (B) *Rhipocephalus phoenix* f. *longifolius*. DLB8074, Carabinero, Mona Island, 50 m. Scale bar = 1.0 cm.

in the Caribbean it has been dredged to depths of 73 m (Taylor 1960). [Additional illustrations: Harvey 1858: pl. 43C; Gepp and Gepp 1911: pl. 21, figs. 183–186.]

***Rhipocephalus phoenix* f. *longifolius* A. Gepp et  
E. Gepp**

FIGURE 66B

*Rhipocephalus phoenix* f. *longifolius* A. Gepp et E. Gepp 1905: 4, pl. 468: fig. 3.

*Puerto Rican Record*: Ballantine et al. 2011a.

*Western Atlantic Distribution*: Belize, North America, Bahamas, Cuba, Guadeloupe, Puerto Rico.

*Type Locality*: Key West, Florida Keys, Monroe County, Florida, USA.

Thalli are lightly calcified, reaching 4.0–7.0 cm tall. Stipes are 2.5 cm long, and the capitula, approximately 4.0 cm long, are about as wide as long. The more or less irregular capitula are composed of loose, drooping blades, 3.0–4.0 cm long and wide. Blade siphons are cylindrical, parallel, dichotomously branched, and laterally fused, 200–250  $\mu$ m in diameter proximally and distally narrowed to 50–100  $\mu$ m.

*Habitat and Comments*: The type specimen is known from less than 1.0 m depth (Gepp and Gepp 1911). Although not common in Puerto Rico, *Rhipocephalus phoenix* f. *longifolius* occurs in deep water, 36–50 m. Littler and Littler (2000) noted *R. phoenix* f. *longifolius* was the most common forma of the species in deepwater habitats, to 40 m. The blades of its capitulum differ from those of *R. phoenix* f. *phoenix* in being loose, longer, and not tightly concentric around the central axis. [Additional illustrations: Gepp and Gepp 1911: pl. 21, fig. 189; Taylor 1960: pl. 20: fig. 2.]

## Udotea J. V. Lamour.

*Udotea* J. V. Lamour. 1812: 186.

Thalli are erect from a rhizoidal base and adherent sand anchor. Algae are substantially calcified with simple stipes bearing a terminal fanlike or funnel-shaped flabellum. The stipe and flabella are composed of dichotomously branched siphons constricted above the dichotomies. In some species, siphons bear lateral branches or simple projections, which constitute a distinctive cortical layer.

**Notes:** Since the pioneering monograph of Gepp and Gepp (1911), monographs focused on the tropical western Atlantic *Udotea* include Littler and Littler (1990b), Collado-Vides et al. (2009), and Acosta-Calderón et al. (2018). Although the genus is recognized morphologically in the field by its characteristic calcified terminal blade, *rbcL* and *tufA* sequence-generated trees (e.g., Kooistra 2002; Lam and Zechman 2006; Verbruggen et al. 2009)

resulted in polyphyletic clades in which characteristics of *Udotea* blade lateral appendages were associated with different clades. Phylogenetic analysis of species of *Udotea* from the Yucatan Peninsula, Mexico, also found that *U. cyanthiformis* var. *flabellifolia* from Campeche was situated in a clade with nonbladed taxa, including *Rhipocephalus phoenix* f. *brevifolius* A. Gepp et E. Gepp from the Florida Keys (with an imbricate blade) and *Penicillus capitatus* from Jamaica (with a capitular brush of filaments). Acosta-Calderón et al. (2018: fig. 85) provided further support that the presence of a calcified blade may not be a diagnostic character of *Udotea*. The phylogenetic separation of *Udotea* species lacking lateral appendages suggests that these uncorticated taxa may belong in another genus. Recent studies have resulted in the recognition that some members of the Udoteaceae belong to other known or new genera.

There are 43 species of *Udotea*, as currently defined, recognized worldwide. Twelve of these species and two infraspecific taxa occur from Puerto Rico, including one new variety herein described.

### KEY TO THE UDOTEA SPECIES OF PUERTO RICO

1. Flabellum funnel shaped ..... *U. cyanthiformis*  
Flabellum fan shaped ..... 2
2. Blade a single layer of siphons ..... *U. unistratea*  
Blade, at least toward the base, multistratose ..... 3
3. Blade siphons without lateral appendages ..... 4  
Blade siphons with lateral appendages ..... 6
4. Blades fibrous ..... 5  
Blades not fibrous ..... *U. conglutinata*
5. Blades 3–5 mm thick, blade siphons to 122 µm diam ..... *U. fibrosa*  
Blades 1.0 mm thick; blade siphons to 90 µm diam ..... *U. abbottiorum*
6. Blades with weak to strong concentric bands (zonate); blade siphons less than 70 µm diam ..... *U. caribaea*  
Blades without concentric bands (not zonate); blade siphons greater than 85 µm diam ..... 7
7. Lateral appendages on blade siphons acute and unilaterally placed ..... *U. spinulosa*  
Lateral appendages on blade siphons blunt or truncate ..... 8
8. Lateral blade siphon appendages do not form a continuous outer cortex ..... *U. goreau*  
Lateral blade appendages form a continuous outer cortex ..... 9
9. Lateral blade siphon appendages randomly placed and scattered ..... *U. flabellum*  
Lateral blade siphon appendages generally opposite and closely set ..... 10
10. Lateral blade siphon appendages not branched ..... *U. occidentalis*  
Lateral blade siphon appendages branched ..... 11
11. Thalli solitary; blades wider than tall; bases of flabella cordate ..... *U. dotyi*  
Thalli frequently in clusters; blades taller than wide, base not cordate ..... *U. dixonii*

## *Udotea abbottiorum* D. S. Littler et Littler

FIGURE 67

*Udotea abbottiorum* D. S. Littler et Littler 1990b: 210, fig. 1a–g.

**Puerto Rican Records:** Littler and Littler 1990b; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016; Acosta-Calderón et al. 2018.

**Western Atlantic Distribution:** Belize, Mexico, Panama, North America, Bermuda, Cuba, Puerto Rico, Brazil, Colombia.

**Type Locality:** NW side of westernmost Content Key, Content Keys, Florida Keys, Monroe County, Florida, USA.

Thalli, reaching to 15 cm tall, are attached by a rhizoidal mass and sand anchors. Stipes measure 4.0–7.0 cm long; they are cylindrical below, 2.0–3.0 mm diam, becoming flattened and 4.0–11 mm diam above. Stipe siphons are 70–100 µm diam, constricted above dichotomous divisions. At the surface, stipe siphons possess swollen apices. Flabella are fibrous and narrowly fan shaped, 8.0 cm long, 5.0 cm wide, and 1.0–3.0 mm thick. Younger plants are faintly zonate, which becomes obscured with age. Flabellum siphons are



FIGURE 67. *Udotea abbottiorum*. MAH2064, herbarium specimen: Santurce, San Juan. Scale bar = 1.0 cm. Courtesy New York Botanical Garden.

subparallel, 90–110  $\mu\text{m}$  diam, possess wide-angled dichotomies, and lack lateral projections. Algae are yellow green in color.

*Habitat and Comments:* *Udotea abbottiorum*, described from 5.0 m depth and considered a shallow-water species (Littler and Littler 1990b), is now also known in deeper habitats. In Puerto Rico, the species occurs from 36 to 46 m depths (Ballantine et al. 2016). A specimen, MAH2064 in NY, from 0.3 m depth in Santurce, was designated by Littler and Littler (1990b) as a paratype. [Additional illustrations: Littler and Littler 2000: 423; Acosta-Calderón et al. 2018: figs. 7–11.]

### ***Udotea caribaea* D. S. Littler et Littler**

FIGURE 68

*Udotea caribaea* D. S. Littler et Littler 1990b: 211: fig. 2a–d.

*Puerto Rican Records:* Ballantine et al. 2015, 2016.

*Western Atlantic Distribution:* Belize, Mexico, Panama, North America, Bermuda, Cuba, Martinique, Puerto Rico, Brazil.

*Type Locality:* NW side of mangrove islands of Tobacco Range, Belize Barrier Reef, Belize.



FIGURE 68. *Udotea caribaea*. DLB8455, herbarium specimen: East side Mona Island, 46–55 m. Scale bar = 1.0 cm.



Thalli are 4.0–9.0 cm tall and attached by rhizoidal mass and sand anchors. Stipes measure to 2.5 cm long and 2.0–5.0 mm diam. Medullary stipe siphons are 60–80  $\mu$ m diam, and cortical stipe siphons possess stubby and digitate projections. Flabella are fan shaped, 10 cm wide, 7.0 cm long, and 0.5–1.0 mm thick. The tightly compact flabellar siphons measure 30–50  $\mu$ m diam, possess asymmetrical constrictions above narrow angled dichotomous divisions, and lack lateral projections. Algae are yellow or whitish green in color.

**Habitat and Comments:** Although generally found in shallow water, 1–7 m depths, including mangrove habitats, *Udotea caribaea* in Puerto Rico has been collected only in deep water, dredged off Mona Island from 46 to 55 m depths. Schneider et al. (2010) first established that the species occurs in deep water, at a 50 m depth in Bermuda (Ballantine et al. 2015). [Additional illustrations: Acosta-Calderón et al. 2018: figs. 12–15.]

***Udotea conglutinata* (J. Ellis et Sol.) J. V. Lamour.**

FIGURE 69

*Udotea conglutinata* (J. Ellis et Sol.) J. V. Lamour. 1816: 312.

**Basionym:** *Corallina conglutinata* J. Ellis et Sol. 1786: 125, pl. 25: fig. 7.

**Puerto Rican Records:** As *Udotea conglutinata*: Diaz-Piferrer 1963; Almodóvar and Blomquist 1959; Almodóvar 1964b; Ballantine 1977; Littler and Littler 1990b; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

**Western Atlantic Distribution:** Mexico, Panama, North America, Bermuda, Bahamas, Antigua, Cuba, Guadeloupe, Hispaniola, Jamaica, Puerto Rico, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

**Type Locality:** “Bahama islands.” Note that the type specimen is apparently lost (Howe 1909; Gepp and Gepp 1911), and Littler and Littler (1990b: 214) selected an illustration of Ellis and Solander (1786: pl. 25: fig. 7) as the lectotype following the opinion of Dixon (1960).

Strongly calcified thalli, measuring 10–15 cm tall, are attached by a rhizoidal mass and sand anchors. Stipes reaching 2.5 cm long and 5.0 mm diam are terete proximally, becoming flattened distally. Stipe siphons measure 50–70  $\mu$ m diam with equal constrictions above dichotomous divisions, and digitate apices of lateral appendages form a cortex. Flabella are flat, orbicular or fan shaped, rounded or somewhat reniform, and deeply cordate at maturity with a torulose surface. Flabella measure to 12 cm



FIGURE 69. *Udotea conglutinata*. In situ habit photograph, algal plain, seaward Media Luna Reef, La Parguera, 17 m. Field = approximately 10.0 cm.

long, 11 cm wide, and 1.0–2.0 mm thick. Flabellum siphons, 40–60 µm diam, are smooth with equal constrictions above dichotomous divisions and lack lateral appendages. The blade siphon apices may be contorted and tortuous. Algae are green to ash white in color.

**Habitat and Comments:** *Udotea conglutinata* generally occurs in shallow water on calcareous and rock platforms, sand bottoms, and seagrass beds. It is also known in deeper waters in Puerto Rico from Monito Island to 40 m depths (Littler and Littler 1990b) and is common on Puerto Rican offshore algal plains down to 62 m depths (Ballantine et al. 2016). Elsewhere in the western Atlantic, the species occurs to 52 m depths in Bermuda (Schneider et al. 2010), off the Gulf of Mexico coast of Florida to 55 m (Dawes and Van Breedveld 1969), and in Florida to 60 m depth (Dawes and Mathieson 2008). [Additional illustrations: Harvey 1858: pl. 40C; Gepp and Gepp 1911: pl. 5: figs. 44, 45, pl. 6: fig. 46; Taylor 1960: pl. 20: fig. 3, pl. 25: fig. 5; Littler and Littler 1990b: fig. 3a–f; Acosta-Calderón et al. 2018: figs. 16–20.]

### ***Udotea cyathiformis* Decne. f. *cyathiformis***

FIGURE 70A

*Udotea cyathiformis* Decne. 1842a: 106.

**Puerto Rican Records:** Almodóvar and Blomquist 1961; Ballantine 1977; Almodóvar and Ballantine 1983; Littler and Littler 1990b; Ballantine and Aponte 1997a, 2002.

**Distribution:** Belize, Costa Rica, Panama, Mexico, North America, Bermuda, Bahamas, Barbados, Cuba, Grenadines, Guadeloupe, Hispaniola, Honduras, Jamaica, Martinique, Puerto Rico, U.S. Virgin Islands, Brazil, Venezuela.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Îles des Saintes, Guadeloupe, Lesser Antilles.

Thalli, 6.0–13 cm tall, are calcified and attached by a rhizoidal mass and sand anchors. Stipes are terete, to 2.0 cm long and 1.0–4.0 mm diam. Stipe siphons measure 50–120 µm diam, with lateral digitate appendages that terminate in rounded to blunt apices. Flabella are funnel shaped, 3.0–5.0 cm across, sometimes open on one side. The faintly zonate blades measure 3.0–4.5 (–10) cm long and 0.5–1.0 mm thick. Flabellum siphons are multi-stratose with nearly parallel siphons, measuring 30–70 µm diam. They are dichotomously to trichotomously divided with equal to unequal constrictions at dichotomies and lack corticating projections. Algae are green to whitish green in color.

**Habitat and Comments:** In Puerto Rico, *Udotea cyathiformis* is common in shallow waters to 4.0 m depths in seagrass beds and to 24 m depths in algal plains. [Additional illustrations: Gepp and Gepp 1911: pl. 1, figs. 2, 6, 9; Littler and Littler 1990b: fig. 4; Acosta-Calderón et al. 2018: figs. 22–25.]

### ***Udotea cyathiformis* f. *infundibulum* (J. Agardh) D. S. Littler et Littler**

FIGURE 70D

*Udotea cyathiformis* f. *infundibulum* (J. Agardh) D. S. Littler et Littler 1990b: 216, fig. 5a–e.

**Basionym:** *Udotea infundibulum* J. Agardh 1887: 71.

The forma is newly reported herein from Puerto Rico: DLB3745, between Punta Cerro Gordo and Punta Fraile, Dorado, dredged from R/V *Isla Magueyes*, 40–50 m, collected by D. L. Ballantine and N. E. Aponte, 11.VI.1991; DLB8035 and DLB8054, SE Mona Island, collected by M. Nemeth et al., 13.I.2010 (US Alg. Coll. 218894).

The form differs from *U. cyathiformis* f. *cyathiformis* in the nature of its thin and papery flabellum and in being unistratose, with tightly laterally coherent flabellar filaments that are parallel at the margins. Blade siphons of *U. cyathiformis* f. *infundibulum* are smaller than the other *U. cyathiformis* forms, reported to be 20–40 µm diam. Puerto Rican specimens agree with Littler and Littler's (1990b) account in all respects, including the morphology of stipe siphon appendages, except that flabellar filaments are slightly larger, measuring 30–50 µm diam.

**Habitat and Comments:** The form has been collected only rarely in Puerto Rico, at depths between 40 and 70 m. [Additional illustration: Littler and Littler 1990b: fig. 5.]

### ***Udotea cyathiformis* f. *mesophotica* D. L. Ballant, H. Ruiz, et J. N. Norris f. nov.**

FIGURE 70B,C

*Udotea cyathiformis* f. *mesophotica* D. L. Ballant, H. Ruiz, et J. N. Norris f. nov.

**Holotype:** DLB7971, collected by M. Nemeth et al., 12.I.2010 (US Alg. Coll. 222934), SE Mona Island, 62 m.

**Paratype:** DLB8035, collected by M. Nemeth et al., 13.I.2010 (US Alg. Coll. 2188954), south Mona Island, 70 m.

Thalli are moderately calcified; plant stipes, 2.0–2.5 mm diam, to 3.0–4.0 cm tall, each support a peltate (non-cuplike) flabellum. The flabellum bears conspicuous concentric banding. The flabellum measures 8.0–10 cm diam and is composed of parallel ecorticate filaments that are unistratose for most of their length. The filaments may become separated distally. Flabellar filaments measure 40–50 µm diam and are basally constricted above dichotomies. Stipe filaments measure 40–60 µm diam and bear lateral appendages that terminate in clustered swollen knobs. The new *Udotea cyathiformis* forma is probably phylogenetically closest to f. *infundibulum* above, differing in its peltate habit and also in the morphology of the stipe lateral appendages.

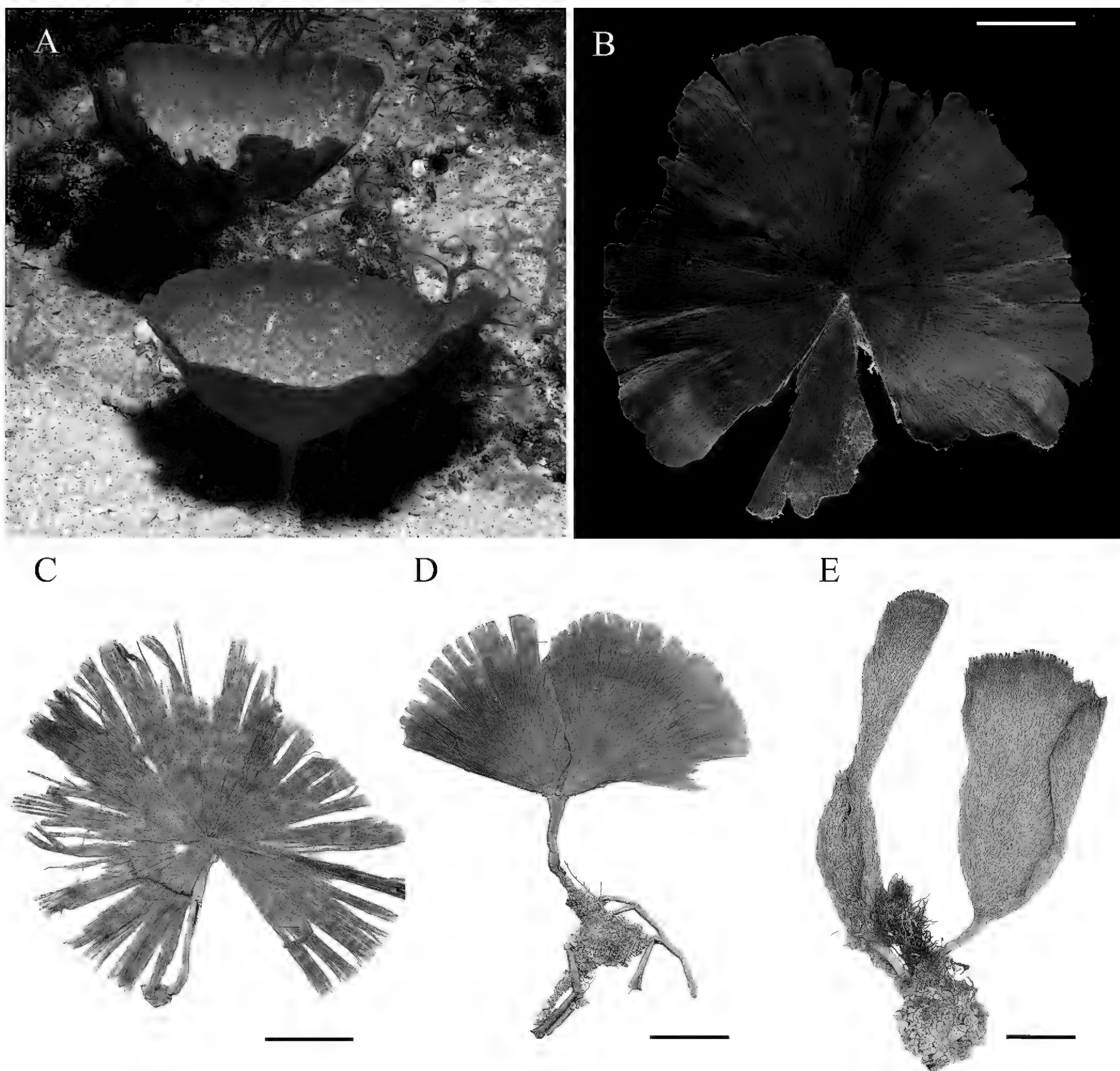


FIGURE 70. *Udotea cyathiformis*. (A) *U. cyathiformis* f. *cyathiformis*. In situ habit photograph from algal plain, seaward of Media Luna Reef, 17 m. Field = approximately 8.0 cm. (B) *U. cyathiformis* f. *mesophotica*. DLB8035: Mona Island, 70 m. Scale bar = 2.0 cm. (C) *U. cyathiformis* f. *mesophotica*. DLB7971, herbarium specimen of the holotype, Mona Island, 62 m. Scale bar = 2.0 cm. (D) *U. cyathiformis* f. *infundibulum*. DLB8102, herbarium specimen, Vieques Island, 30.5 m. Scale bar = 2.0 cm. (E) *U. cyathiformis* f. *sublittoralis*. MD-P3022, herbarium specimen: Manatí, Puerto Rico. Scale bar = 1.0 cm. Courtesy New York Botanical Garden.

***Udotea cyathiformis* f. *sublittoralis* (W. R. Taylor)  
D. S. Littler et Littler**

FIGURE 70E

*Udotea cyathiformis* f. *sublittoralis* (W. R. Taylor) D. S. Littler et Littler 1990b: 216, fig. 6a–e.

*Basionym*: *Udotea sublittoralis* W. R. Taylor 1928: 91, pl. 8: fig. 16, pl. 9: figs. 8, 9.

*Puerto Rican Records*: As *Udotea sublittoralis*: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983. As *Udotea cyathiformis* f. *sublittoralis*: Littler and Littler 1990b.

*Western Atlantic Distribution*: Belize, Costa Rica, Mexico, Panama, North America, Bahamas, Cuba, Martinique, Puerto Rico, St. Eustatius, Brazil.

*Type Locality*: Garden Key, Dry Tortugas, Monroe County, Florida, USA.

Flabella are cup-shaped, lightly calcified, and fibrous, sometimes with faint concentric zones. The flabella are usually wider (up to 4.0 cm in diameter) than tall (up to 3.5 cm) and 2.0–3.0 mm

thick, with siphons interwoven to form a fibrous cup with multi-stratose blade margins. Flabellum siphons are 100–150 µm diam with wide dichotomies, not parallel or laterally adherent. The forma differs from the nominate species by its thicker fibrous flabellum.

*Habitat and Comments*: *Udotea cyathiformis* f. *sublittoralis* occurs in Puerto Rico in shallow water to 4 m depths in protected environments such as seagrass beds and mangroves. The nomotypical forma was from 12 m depth (Littler et Littler 1990b). A specimen (Diaz Piferrer3022) collected at Playa Tortuga, Manatí, 1–2 m depth, in 1962 was included as a paratype of the form. Presumed to be part of a continuum of forms of *U. cyathiformis* var. *cyathiformis*, *U. cyathiformis* f. *sublittoralis* differs from the other taxonomic forms by its lightly calcified, thicker, tough, fibrous cup-shaped blades of interwoven blade siphons. [Additional illustrations: Taylor 1960: pl. 22: fig. 6; Littler and Littler 1990b: fig. 6a–e; Acosta-Calderón et al. 2018: figs. 26, 27.]

***Udotea dixonii* D. S. Littler et Littler**

FIGURE 71

*Udotea dixonii* D. S. Littler et Littler 1990b: 220, fig. 8a–f.

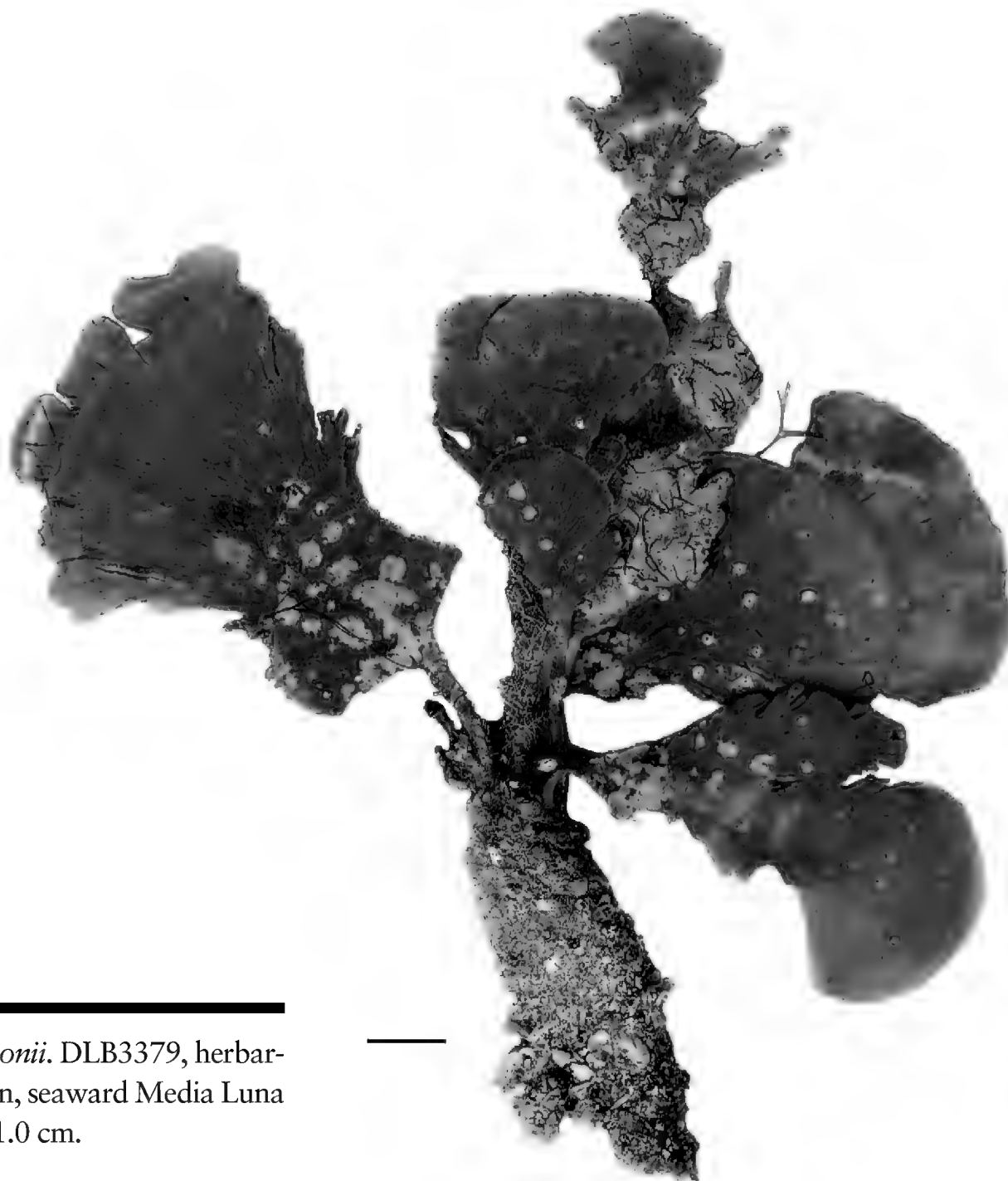


FIGURE 71. *Udotea dixonii*. DLB3379, herbarium specimen: Algal plain, seaward Media Luna Reef, 17 m. Scale bar = 1.0 cm.



*Puerto Rican Records:* Littler and Littler 1990b; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution:* Belize, Mexico, Panama, North America, Cuba, Hispaniola, Martinique, Nicaragua, Puerto Rico, St. Eustatius, Brazil, Venezuela.

*Type Locality:* East side of Curlew Cay (now Curlew Bank), Belize Barrier Reef, Belize.

Thalli, reaching up to 21 cm tall, are strongly calcified. They are attached by a rhizoidal mass and sand anchors and typically occur as individuals or in groups of 2 to 5. Stipes measure 2.0–6.0 cm long and 2.0–3.0 mm diam. Stipe siphons are 30–60  $\mu$ m diam and are unequally constricted at dichotomies. They are covered by 2, often paired, vertical rows of lateral appendages that terminate in dichotomously divided, stubby, closely intertwined digitate projections (making them difficult to separate, even after decalcification). The flat lobed flabella are 6.0–12 cm long, 4.0–10 cm wide, and 0.2–0.8 mm thick. They possess distinct concentric zones and are bistratose at the outer margin and multistratose proximally. Blade siphons are cylindrical or slightly moniliform, 20–35  $\mu$ m diam, and densely covered with 2, often paired, vertical rows of lateral appendages. The siphon appendages are widely spreading or clustered in multiple, swollen knobs or short projections. Algae are yellow green in color.

*Habitat and Comments:* *Udotea dixonii* is typically found in deepwater habitats, occurring from 40 to 60 m depths in Puerto Rico (Ballantine et al. 2016). Described from the Belize Barrier Reef at 46 m depth (Littler and Littler 1990b), *U. dixonii* is also reported from 38 m off the east (Atlantic) coast of Florida (Hani-sak and Blair 1988); from 50 to 56 m on Campeche Banks, Gulf of Mexico (Mateo-Cid et al. 2013); and to 55 m depths in Cuba (Suarez et al. 2015). [Additional illustrations: Littler and Littler 1990b: 220, fig. 8a–f, 2000: figs. p. 229; Acosta-Calderón et al. 2018: figs. 35–40.]

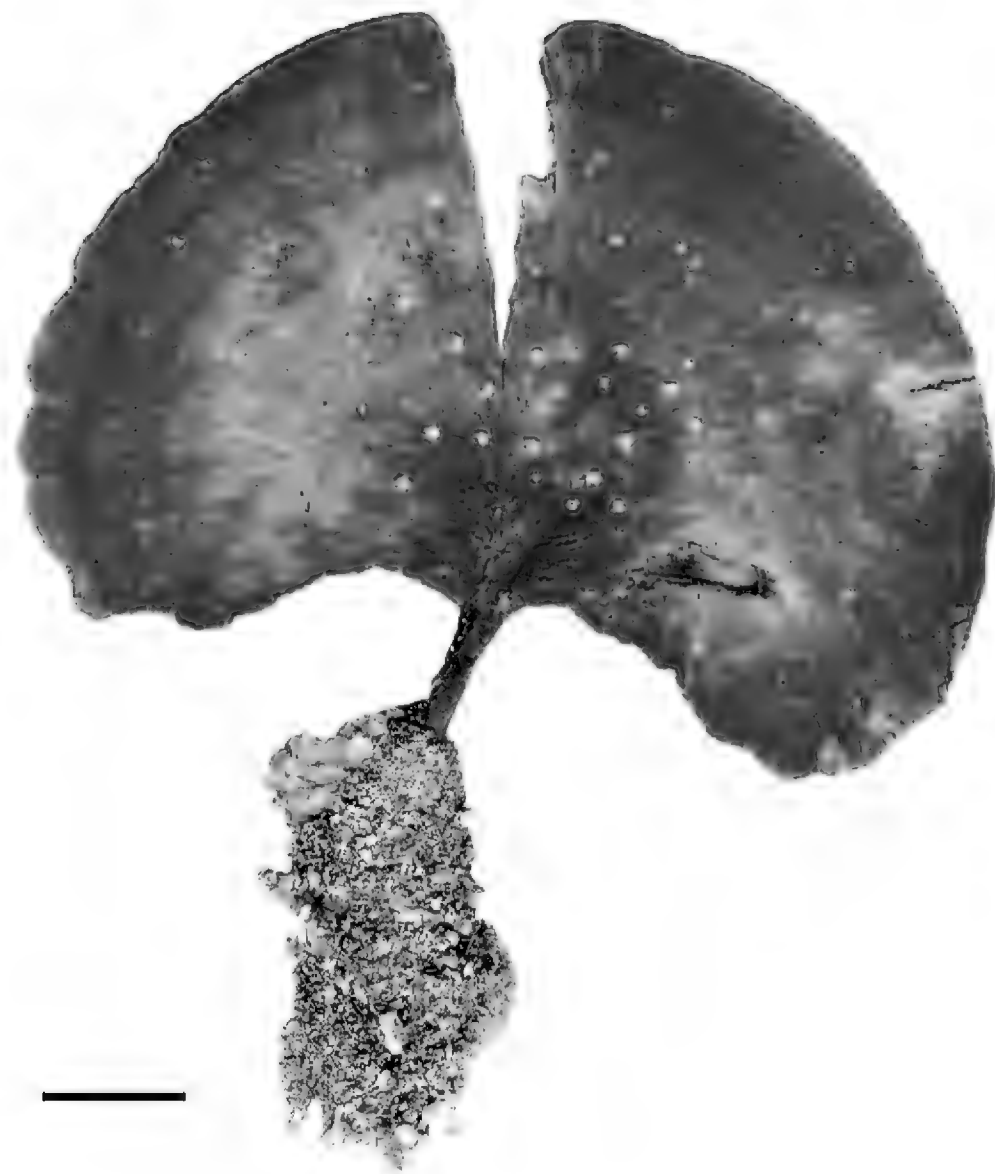
### ***Udotea dotyi* D. S. Littler et Littler**

FIGURE 72

*Udotea dotyi* D. S. Littler et Littler 1990b: 223, figs. 9d,e, 10a–f.

*Puerto Rican Records:* Littler and Littler 1990b; Ballantine and Aponte 2002.

*Western Atlantic Distribution:* Mexico, Panama, North America, Cuba, Hispaniola, Honduras, Puerto Rico.



**FIGURE 72.** *Udotea dotyi*. DLB3378, herbarium specimen: Algal plain, seaward Media Luna Reef, 17 m. Scale bar = 1.0 cm.

*Type Locality:* Tobago Cays, Southern Grenadines, Grenadines, Lesser Antilles.

Thalli, measuring to 23 cm tall, are attached by a rhizoidal mass and sand anchors. Stipes are relatively short, up to 2.0 cm tall and to 4.0 mm diam. The stipe siphons measure 70–100  $\mu$ m diam with long-stalked lateral appendages, terminating in numerous rounded tips. Flabella are large, often wider (to 13 cm) than long (8.0 cm), and 0.5–1.0 mm thick. The flabella are sparingly lobed, flat, and paddle shaped, with a deeply cordate lower margin in mature plants. The flabella are multistratose throughout, with faint concentric zonation. Unequally divided flabellum siphons are oval, 60–80  $\mu$ m on flattened sides and 40–50  $\mu$ m wide at marginal edges, with dense subopposite rows of short, to 200  $\mu$ m long, appendages. Algae are dark gray green in color.

*Habitat and Comments:* *Udotea dotyi* is uncommon in Puerto Rico, occurring at moderate depths in sandy habitats. The holotype was collected on sand-covered dead coral at 12 m depth (Littler and Littler 1990b). [Additional illustrations: Littler and Littler 1990b: fig. 10a–f, 2000: 427; Acosta-Calderón et al. 2018: figs. 43–44.]

***Udotea fibrosa* D. S. Littler et Littler**

FIGURE 73

*Udotea fibrosa* D. S. Littler et Littler 1990b: 226, fig. 11a–d.

*Misapplied Name:* *Udotea sublittoralis*: Almodóvar and Ballantine 1983.

*Puerto Rican Records:* Newly reported from Puerto Rico: DLBsn, 1.0 m, Jobos Beach, near Aguadilla (23.II.1974, US Algal Coll. 218751), identified as “*U. sublittoralis*,” annotated as *Udotea fibrosa* by D. S. Littler.

*Western Atlantic Distribution:* Belize, Costa Rica, North America, Cuba, Hispaniola, Jamaica, Martinique, Puerto Rico.

*Type Locality:* In sand, about 50 m from shore, 0.5 m depth; shallow reef flat off east side of Carrie Bow Cay, Belize Barrier Reef, Belize.

Thalli measure to 6.0 cm tall and are attached by a rhizoidal mass and sand anchors. Stipes are stout and rigid, to 1.0 cm long and 5.0 mm diam. The stipe siphons, 120–180  $\mu\text{m}$  diam, are dichotomously divided with unequal constrictions at dichotomies and bear lateral projections that terminate in short dichotomously divided rounded to bulbous tips. Nonzonate, frequently asymmetrical flabella are multistratose and fibrous; they are fan shaped, frequently lobed, longer than broad, 11 cm long and 3.0–5.0 mm thick. Dichotomously divided flabellum siphons are moniliform, 100–150  $\mu\text{m}$  diam, with unequal constrictions at dichotomies and lacking appendages. Algae are dull dark green, lighter green when heavily calcified.

*Habitat and Comments:* Uncommon in Puerto Rico, *Udotea fibrosa* occurs in very shallow water. The type species was collected in sand at 0.5 m depth (Littler and Littler 1990b). Despite the similarity of their fibrous flabella, *U. fibrosa* possesses a

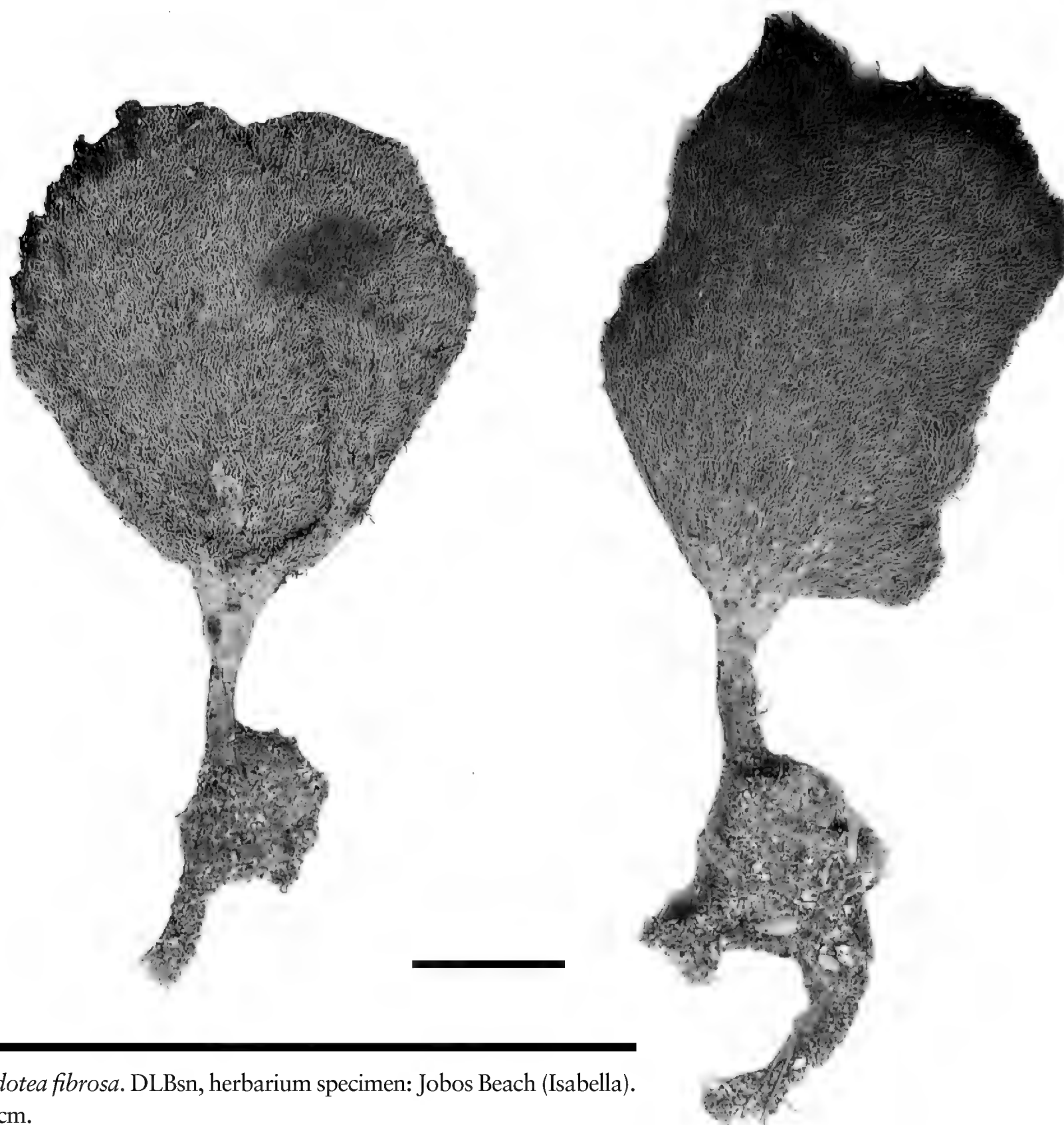


FIGURE 73. *Udotea fibrosa*. DLBsn, herbarium specimen: Jobos Beach (Isabella). Scale bar = 1.0 cm.

thicker blade (3.0–5.0 versus 2.0–3.0 mm) than *U. cyathiformis* f. *sublittoralis* in addition to possessing a larger blade siphon diameter, 122 versus 70  $\mu\text{m}$  (Littler and Littler 1990: 427). [Additional illustrations: Acosta-Calderón et al. 2018: figs. 435–448.]

***Udotea flabellum* (J. Ellis et Sol.) M. Howe**

FIGURE 74

*Udotea flabellum* (J. Ellis et Sol.) M. Howe 1904: 94, pl. 6.

*Basionym:* *Corallina flabellum* J. Ellis et Sol. 1786: 124, pl. 24A–D. [Note that plate 24 is a lectotype illustration selected by Littler and Littler (1990b: 229).]

*Puerto Rican Records:* As *Udotea flabellum*: Almodóvar and Blomquist 1959; Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar 1962, 1964b, 1971; Almodóvar and Pagán 1971; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution:* Belize, Costa Rica, Mexico, Panama, North America, Bermuda, Bahamas, Barbados, Antigua, Cayman Islands, Cuba, Dominica, Grenadines, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, St. Barthélemy, St. Eustatius, St. Kitts,

St. Lucia, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* West Indies.

Thalli reach 30 cm tall, arising from large bulbous anchors of rhizoidal filaments and adherent sediment; plants are moderately calcified. Stipes are simple, 2.0–4.0 cm long and 5.0–7.0 mm diam; they are terete below and somewhat flattened above. Stipe siphons, 20–80  $\mu\text{m}$  diam, are not constricted above dichotomies and possess projections that terminate in compact clusters of small, rounded apices. Flabella are fan shaped, often reniform, and cordate below. The flabella are strongly zonate (generally of more or less distinct concentric lines) and measure 5.0–21 cm long, 5.0–30 cm broad, and 0.8–1.5 mm thick. Flabella frequently become proliferous and may later become highly divided with many overlapping lobes. Blade siphons lack constrictions or sometimes have slightly unequal constrictions above sparse dichotomies. The siphons measure 30–50  $\mu\text{m}$  in diameter and bear irregularly spaced, densely branched, long-stemmed lateral appendages that terminate in crowded, short, dichotomously branched projections with rounded truncate and thickened apices. Algae are gray green in color.

*Habitat and Comments:* In Puerto Rico, *Udotea flabellum* is generally found in sandy, shallow-water habitats to 10 m depths

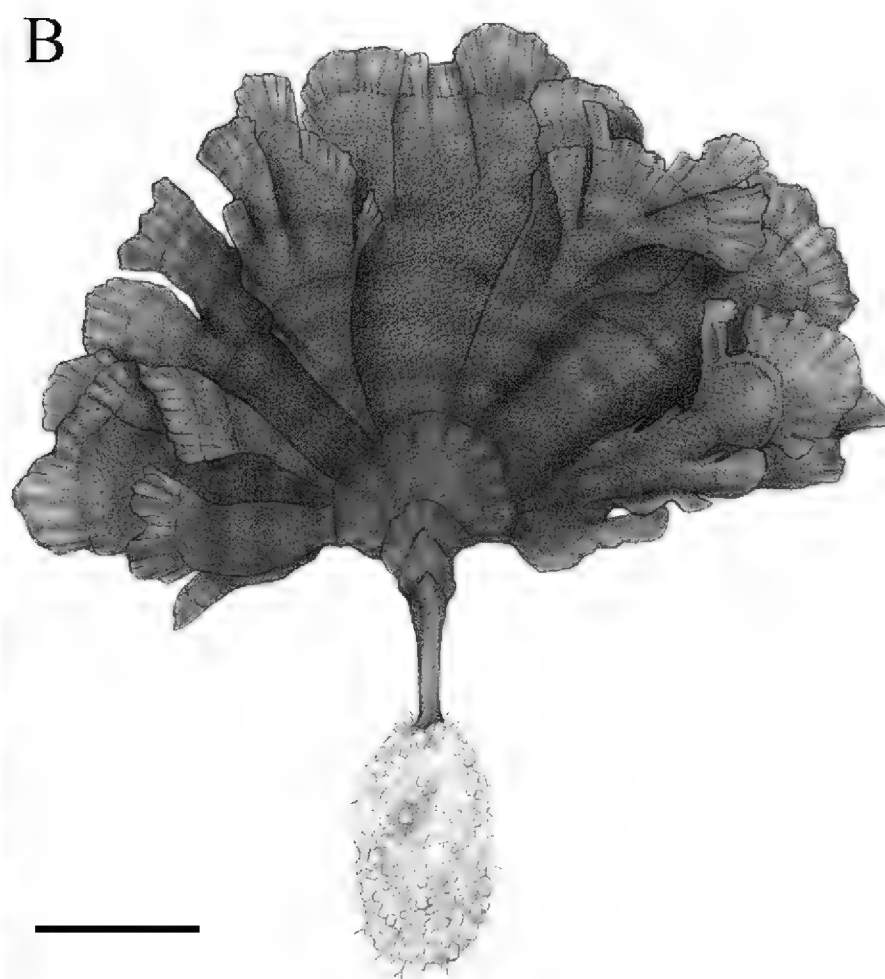
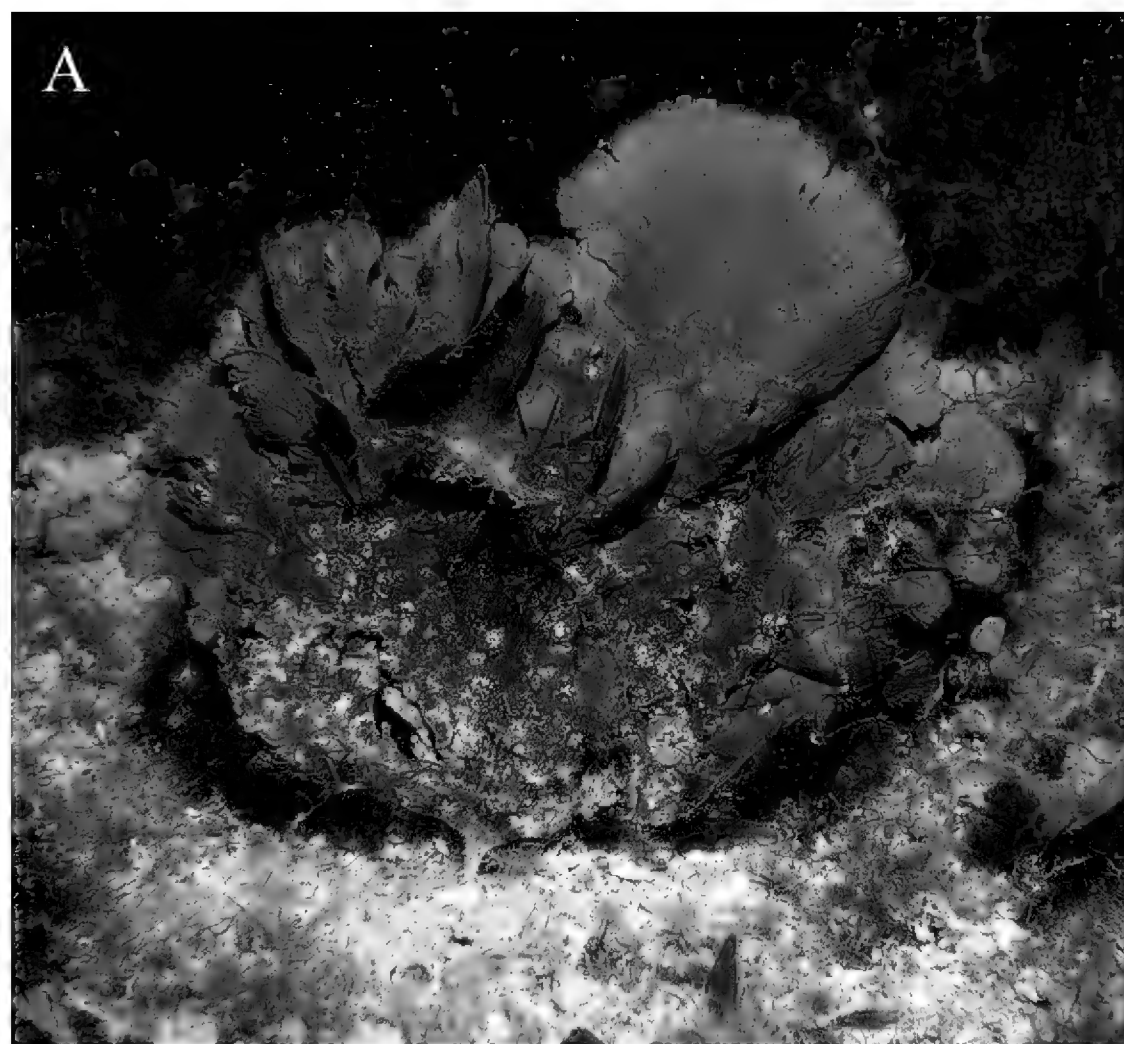


FIGURE 74. *Udotea flabellum*. (A) In situ habit photograph from seaward of Media Luna Reef, 17 m. Field = approximately 30 cm. (B) Pencil and watercolor, from live specimen. Scale bar = 2.0 cm.

as well as in offshore algal plains. *Udotea flabellum* has also been reported from deep water in Puerto Rico at 36–60 m depths (Ballantine et al. 2016). [Additional illustrations: Gepp and Gepp 1911: pl. 1, fig. 26; Littler and Littler 1990b: fig. 12, 2000: 230; Acosta-Calderón et al. 2018: figs. 52–55.]

***Udotea goreau* D. S. Littler et Littler**

FIGURE 75

*Udotea goreau* D. S. Littler et Littler 1990b: 229, figs. 14a–h.

*Puerto Rican Records:* Littler and Littler 1990b; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Cuba, Jamaica, Puerto Rico.

*Type Locality:* West Runaway Bay, Jamaica; holotype specimen (NY).

Thalli reach 12 cm tall and are heavily calcified. Stipes are slender, to 1.5 cm long and to 1.0 mm diam. Stipe siphons measure 150–180  $\mu$ m diam and possess branched, generally unilateral appendages that terminate in dichotomously divided blunt tips. Flabella are fan shaped and subtly zonate, measuring 7.5 cm long and 9.0 cm wide. The distal two-thirds of the flabellum are unistratose, 0.1–0.2 mm thick. The proximal flabellum portions are multistratose, to 1.0 mm thick. Flabellum siphons measure 100–150  $\mu$ m diam, possess unequal constrictions above the dichotomies, and are parallel and interlocked to each other by short, simple to branched, papillae-like laterals in double vertical rows and by heavy calcium carbonate deposits. Algae are grayish green in color when dried.

*Habitat and Comments:* *Udotea goreau* is an alga of intermediate (17–24 m) depths, having been collected in offshore algal plains in southwest Puerto Rico. The holotype was collected in sand, on a fore-reef slope, at 40 m depth (Littler and Littler 1990b); Puerto Rican paratype specimens annotated by D. S. Littler are 1.5 km seaward of Media Luna Reef (US Alg. Coll. 91656) and seaward of Margarita Reef (DLB530; US Alg. Coll. 161731). The flabellum dimensions calculated from Littler and Littler's (1990b) figure 14a are substantially greater than those of the above referred to herbarium specimens. The Puerto Rican specimens measured to a maximum height of 3.6 cm, with maximum flabellum dimensions of 2.9 cm long and 1.6 cm wide.

***Udotea occidentalis* f. *radiata* D. L. Ballant. et J. N. Norris f. nov.**

FIGURE 76

*Udotea occidentalis* f. *radiata* D. L. Ballant. et J. N. Norris

*Misapplied Name:* As *Udotea wilsoni* A. Gepp, E. Gepp, et Howe: Almodóvar and Ballantine 1983. As *Udotea occidentalis*: Littler and Littler 1990b; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.



FIGURE 75. *Udotea goreau*. DLB655, herbarium specimen: Seaward Media Luna Reef, 17 m. Scale bar = 0.5 cm.



*Holotype*: DLB3678, collected by D. L. Ballantine and V. Rosado, 16.XI.1979 (US Algae Coll. 218694), seaward Caja de Muertos Island, 30–60 m offshore in seagrass bed, 1.0–2.0 m.

*Paratypes*: DLBsn, collected by V. Rosada, 14.VII.1975 (US Algae Coll. 218700), seaward Caja de Muertos Island, 30–60 m offshore in seagrass bed, 1.0–2.0 m; DLB8157, collected by L. R. Almodóvar and V. Rosado, 8.XI.1977 (US Algae Coll. 218692), seaward Caja de Muertos Island, 30–60 m offshore in seagrass bed, 1.0–2.0 m.

*Western Atlantic Distribution*: Puerto Rico.

*Type Locality*: Isla Caja de Muertos, Ponce, Puerto Rico.

Thalli are to 10 cm tall and well calcified. Stipes are simple and terete, measuring to 1.0 cm tall and 2.0 mm diam. Stipe siphons are dichotomously branched, 40–70  $\mu\text{m}$  diam with long-stalked lateral appendages that terminate in numerous stubby, rounded apices. Flabella, radiating from a central axis, are more or less proliferous. The flabella are zonate, fan shaped, and obovate above, with a cuneate or deeply cordate base. The proliferous newer bladelike lobes measure 8.0 cm long and 8.0 cm wide; they are papery thin.

Flabellum siphons, 20–50  $\mu\text{m}$  diam, bear capitate, closely forked lateral branchlets, terminating in abundant rounded prominences. Algae are gray below, greener above in color.

*Habitat and Comments*: *Udotea occidentalis* f. *radiata* is typically a shallow-water alga that also occurs in moderately deep water, 9–40 m, on sandy bottoms; however, the species is known to a maximum depth of 70 m in Puerto Rico (Ballantine et al. 2016). In Puerto Rico, this taxon was first reported as *U. occidentalis* A. Gepp, E. S. Gepp 1911 from Caja de Muertos, Ponce, Puerto Rico, in shallow water to 3.0 m depth on a sandy bottom. However, these plants were very highly proliferous, with flabella oriented in multiple planes. This flabellum arrangement is similar to that seen in *Udotea wilsonii* (see Gepp and Gepp 1911: pl. 7 fig. 66). The two taxa differ, however, in that *U. occidentalis* has closely placed blade siphons, 20–40  $\mu\text{m}$  in diameter, bearing unique, swollen lateral appendages with 6–20 knob-like, blunt, low, rounded apices on blade siphons, versus *U. wilsonii*, which has larger blade siphons, 40–80  $\mu\text{m}$  in diameter, bearing ditrichotomously divided shorter, lateral appendages (not knobby), 25–90  $\mu\text{m}$  long (Littler and Littler 1990b). *Udotea occidentalis* also

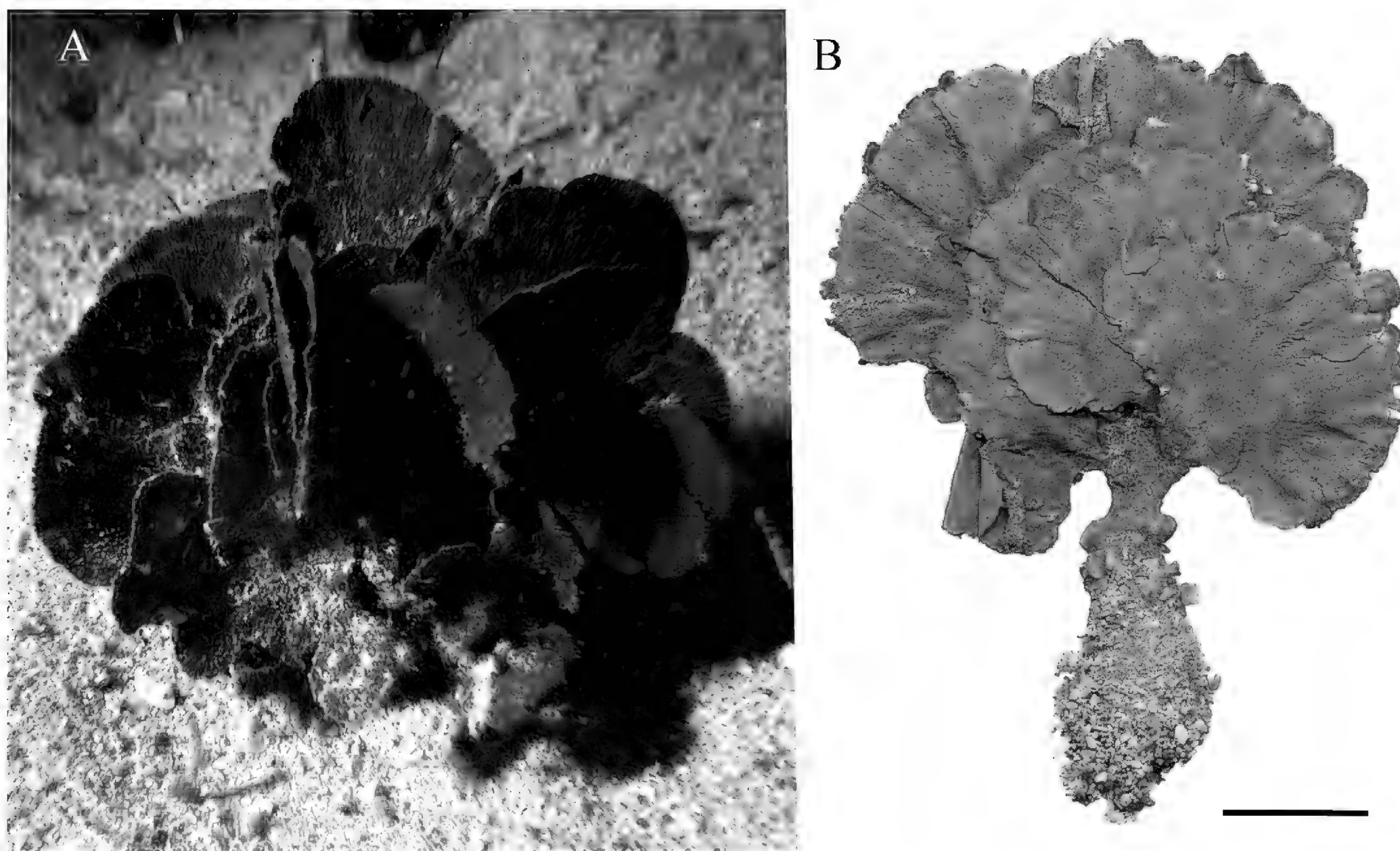


FIGURE 76. *Udotea occidentalis* f. *radiata*. (A) In situ habit photograph from leeward Isla Caja de Muertos, Ponce, 3.0 m. Field = approximately 6.0 cm. (B) Herbarium specimen of the holotype (DLB3678). Scale bar = 1.0 cm.

possesses closely placed flabellum siphons that form a dense continuous cortex that further differs from *U. wilsonii*, which does not. [Additional illustration: as *Udotea occidentalis*, Almodóvar and Ballantine 1983: fig. 2.]

***Udotea spinulosa* M. Howe**

FIGURE 77

*Udotea spinulosa* M. Howe 1909: 97, pl. 4: fig. 2, pl. 8: figs. 1–7.

*Puerto Rican Records:* Almodóvar 1970; Almodóvar and Ballantine 1983; Littler and Littler 1990b; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution:* Mexico, North America, Bahamas, Cuba, Jamaica, Puerto Rico, St. Eustatius, U.S. Virgin Islands, Brazil, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Bimini Harbor, South Bimini, Bimini Islands, Bahamas.

Heavily calcified thalli measure to 8.0 cm tall. Stipes are cylindrical below, becoming flattened above, 1.0–2.0 cm long and 1.0–2.0 mm diam. Stipe siphons are 80–120  $\mu$ m diam, possess equal constrictions above the dichotomies, and bear lateral appendages terminating in long, digitate acute projections. Flabella are obovate or become variously shaped; they are very thin and possess faint concentric zonation. The flabella measure 4.0–6.0 cm long and 4.0–8.0 cm wide and are less than 0.8 mm thick. The flabella are multistratose but become unistratose at the distal margins. Medullary flabellum siphons measure 46–84  $\mu$ m diam with corticating appendages, 55–160  $\mu$ m long, set in a single row, these with 2–8 acuminate prongs. Algae are green to whitish in color.

*Habitat and Comments:* In Puerto Rico, *Udotea spinulosa* chiefly occurs on moderately deepwater sand plains; the species is commonly collected at the Media Luna algal plain, 17 m, and has also been collected on the north Puerto Rican coast, to 46 m (Ballantine et al. 2016). The type species, however, is from a sandy bottom near the low-water mark (Howe 1909). [Illustration: Gepp and Gepp 1911: pl. 1: fig. 12, pl. 6: fig. 55; Littler and Littler 1990b: fig. 19; Acosta-Calderón et al. 2018: figs. 74–76.]

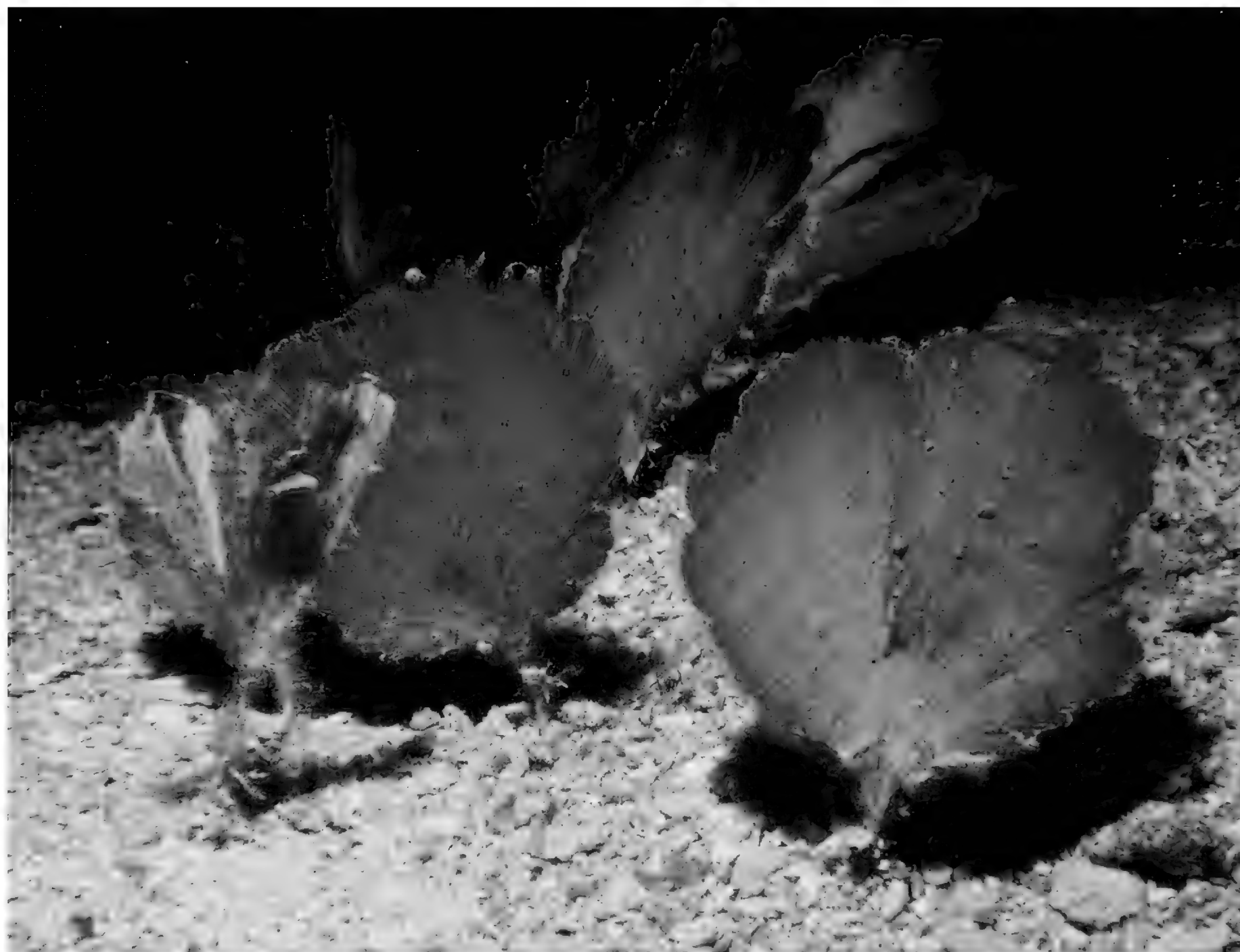


FIGURE 77. *Udotea spinulosa*. In situ habit, seaward of Media Luna Reef, 17 m. Field = approximately 15 cm.

***Udotea unistratea* D. S. Littler et Littler**

FIGURE 78

*Udotea unistratea* D. S. Littler et Littler 1990b: 240, figs. 9f, 21a–d.

*Puerto Rican Records*: Ballantine et al. 2011a, 2016.

*Western Atlantic Distribution*: Belize, Mexico, North America, Bahamas, Cuba, Jamaica, Martinique, Puerto Rico, U.S. Virgin Islands.

*Type Locality*: East side of Carrie Bow Cay, Belize Barrier Reef, Belize.

Thalli, to 7.0 cm tall, are attached to the substrata by small fibrous rhizoids. Stipes measure 1.0–5.0 cm long and 1.0 mm diam but are reported to be occasionally absent (Littler and Littler 1990b: 243). Stipe siphons are 80–130  $\mu$ m diam and bear short, dichotomously branched, blunt projections. Flabella are unistrate, ecorticate, concave or flat with faint concentric lines present, measuring 3.3 cm long, 4.5 cm wide, and 0.1–0.4 mm thick. Blade siphons are 100–240  $\mu$ m in diam, with equal constrictions above dichotomies. The siphons are parallel to each other and are laterally adhered by calcium carbonate and lack lateral appendages. Algae are olive green in color.

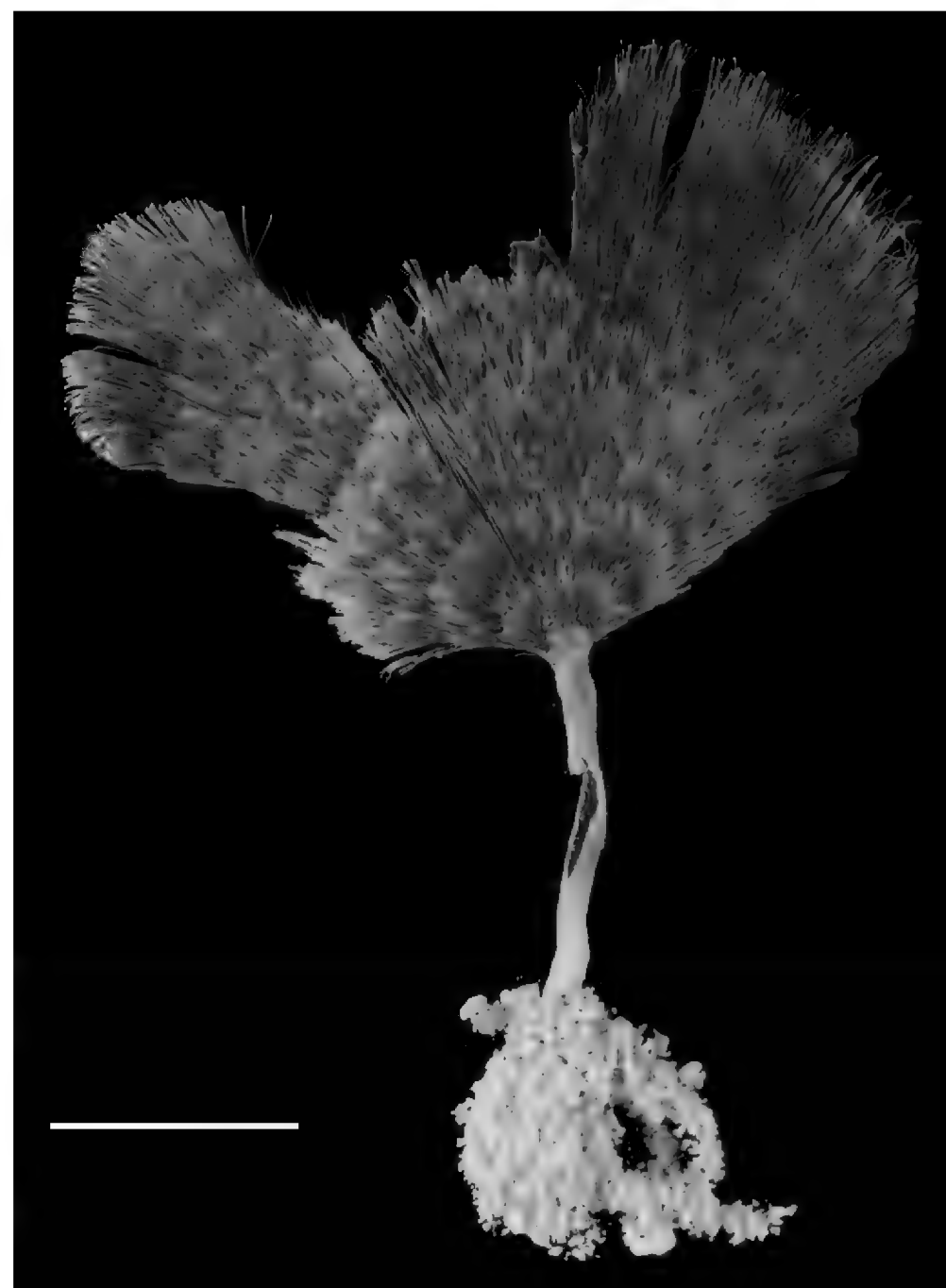
*Habitat and Comments*: *Udotea unistratea* is considered an intermediate depth to deepwater species, occurring from 24 to 46 m depths on hard substrata (Littler and Littler 1990b) and 50–56 m depths from Campeche Banks (Mateo-Cid et al. 2013). Puerto Rico specimens were collected to a depth of 70 m (Ballantine et al. 2016). [Additional illustrations: Acosta-Calderón et al. 2018: figs. 77–78.]

**CLADOPHORALES HAECKEL****ANADYOMENACEAE KÜTZ.*****Anadyomene* J. V. Lamour. nom. cons.**

*Anadyomene* J. V. Lamour. 1812, nom. cons.

**KEY TO THE ANADYOMENE SPECIES OF PUERTO RICO**

- |   |                        |
|---|------------------------|
| 1. Interstitial cells randomly oriented .....                 | 2                      |
| Interstitial cells generally parallel .....                   | 3                      |
| 2. Outer margin composed of small cells .....                 | <i>A. saldanhae</i>    |
| Outer margin composed of elongate vein cells .....            | <i>A. howei</i>        |
| 3. Plant margins irregularly lacerate .....                   | <i>A. lacerata</i>     |
| Plant margins mostly entire .....                             | 4                      |
| 4. Rhizoids limited to proximal portions of the thallus ..... | <i>A. stellata</i>     |
| Rhizoids issued from the entire blade surface .....           | <i>A. rhizoidifera</i> |



**FIGURE 78.** *Udotea unistratea*. DLB8047, herbarium specimen: Vieques, El Seco, 70 m. Scale bar = 2.0 cm.

*Anadyomene* is foliaceous and inconspicuously stalked, attached by rhizoids from the lower stalk and rib cells. Loose to dense clusters of blades are formed by polychotomously branching flabellate series of vein cells that possess intercalary cells between them. Cells are multinucleate; chloroplasts possess a single pyrenoid. There are four Puerto Rican *Anadyomene* species; a total of 15 species are recognized worldwide.



**Anadyomene howei D. S. Littler et Littler**

FIGURE 79

*Anadyomene howei* D. S. Littler et Littler 1991: 103–105, figs. 1–5.

**Puerto Rican Records:** The species is newly recorded for Puerto Rico herein: DLB8462 (US Alg. Coll. 235438) was collected at a depth of 0.5 m at Sardinera, Mona Island.

**Western Atlantic Distribution:** Bahamas, Bermuda, Puerto Rico.  
**Type Locality:** Great Ragged Island, Bahamas.

The entire frond grows prostrate and measures to 3.5 cm in the longest dimension. Veins are composed of single uniseriate series of cells, measuring 380–700  $\mu\text{m}$  long and 220–300  $\mu\text{m}$  diam. Veins are terminated by 2–5 vein branches distally. Vein basal cells are attached by tenacula. Interstitial cells measure 100–150  $\mu\text{m}$  diam. Frond margins are smooth, made up of elongate vein cells. Algae are pale yellow green in color.

**Habitat and Comments:** *Anadyomene howei* is very uncommon in Puerto Rico. As was the case for the Puerto Rican specimen, the holotype was collected in less than 1.0 m of water. Schneider and Lane (2007) reported the species at depths of 12–29 m from Bermuda.

**Anadyomene lacerata D. S. Littler et Littler**

FIGURE 80

*Anadyomene lacerata* D. S. Littler et Littler 1991: 105, figs. 6–14.

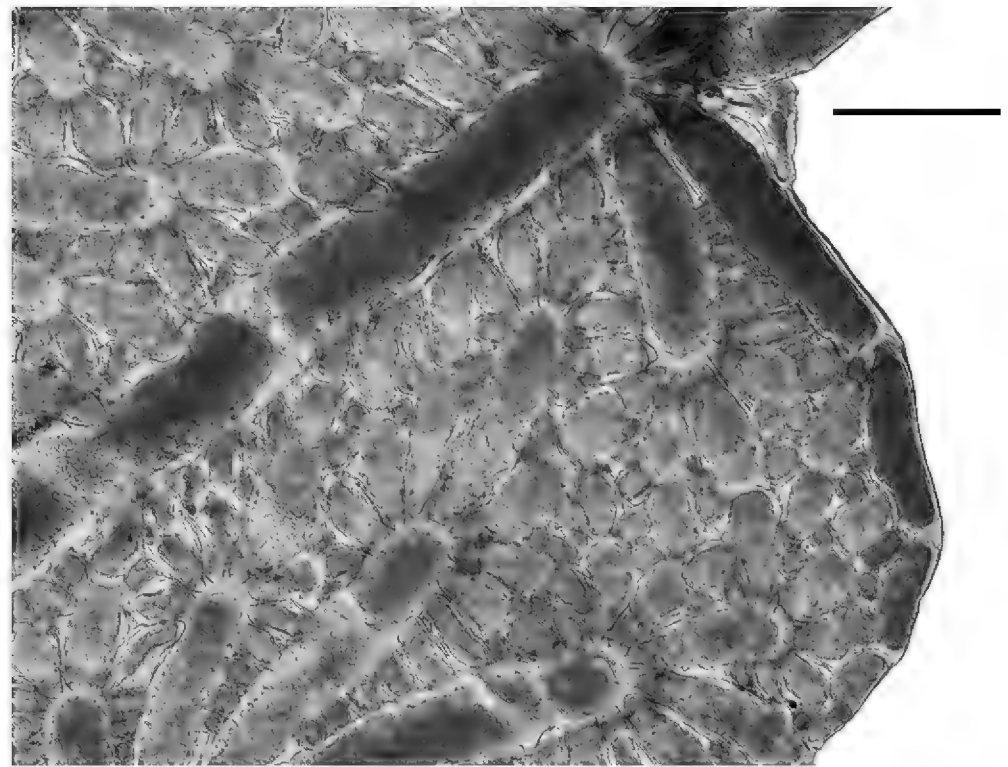
**Puerto Rican Records:** Littler and Littler 1991; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

**Western Atlantic Distribution:** Mexico, Bermuda, North America, Puerto Rico, Brazil.

**Type Locality:** West side of Isla Monito, northwest of Isla de Mona, Puerto Rico.

Fronds are peltate to 6.0 cm tall and 10 cm wide; they are anchored by numerous thick-walled rhizoids that extend from stipe filaments. Blades are deeply cordate at their bases and possess lacerate margins. Veins are composed of 1–3 elongate cells, 200–2,800  $\mu\text{m}$  long and 160–320  $\mu\text{m}$  diam, terminated by 2–6 polychotomous branches. The bases of vein cells are forked and straddle the apex of the proximal cells. Interstitial cells are small and perpendicular to the main vein, lying parallel to one another. Interstitial cells are generally dumbbell shaped or H shaped. Algae are pale yellow green in color.

**Habitat and Comments:** The first record of the species in Puerto Rico is based on the holotype collection by D. S. Littler and M. Littler (1991) on pebbles in a sand plain at 40 m depth. *Anadyomene lacerata* is a deepwater species known in Puerto Rico from 40 to 62 m depths (Ballantine et al. 2016), in the Bahamas from 61 m depths (Norris and Olsen 1991), and in Brazil from 45 to 65 m (Alves et al. 2011) and dredged to 180



**FIGURE 79.** *Anadyomene howei*. DLB8462: Sardinera, Mona Island, 0.5 m. Photomicrograph showing arrangement of marginal vein and interstitial cells. Scale bar = 200  $\mu\text{m}$ .

m depths (Yoneshigue-Valentin et al. 2005, 2006). [Additional illustrations: Alves et al. 2011: figs. 1–11.]

**Anadyomene rhizoidifera A. B. Joly et Pereira**

FIGURE 81

*Anadyomene rhizoidifera* A. B. Joly et Pereira 1973: 79–80, figs. 1–7.

**Puerto Rican Records:** The species is newly recorded for Puerto Rico herein: DLB8468, east side of Mona Island, 46–55 m.

**Western Atlantic Distribution:** Puerto Rico, Brazil, Venezuela.

**Type Locality:** Pernambuco: Cabo, Praia do Gaibu, Brazil.

Blades, occurring in small tufts, were initially reported to be 2.8 cm tall and 4.0 cm wide. Algae are basally attached by rhizoids, frequently entangled to form a stipe-like structure. Blades possess entire margins, consisting of small spherical cells. Veins, 1.3–3.4 mm long, are typically composed of a single elongate cell, occasionally 2, that is terminally polychotomously branched, giving rise to 2–4 vein cells. Interstitial cells are arranged in parallel series and are H shaped. Rhizoids are abundant on the blade, initiated from the base of daughter vein cells. The rhizoids run parallel to parent vein cells. Algae are dark green in color.

**Habitat and Comments:** The single Puerto Rican plant measured 7.5 cm in the largest dimension. The blade of the Puerto Rican plant measured up to 250  $\mu\text{m}$  and 1–3(–4) cells thick. Following its initial report, the species has been subsequently recorded from Brazil (Alves et al. 2011) and Los Roques,



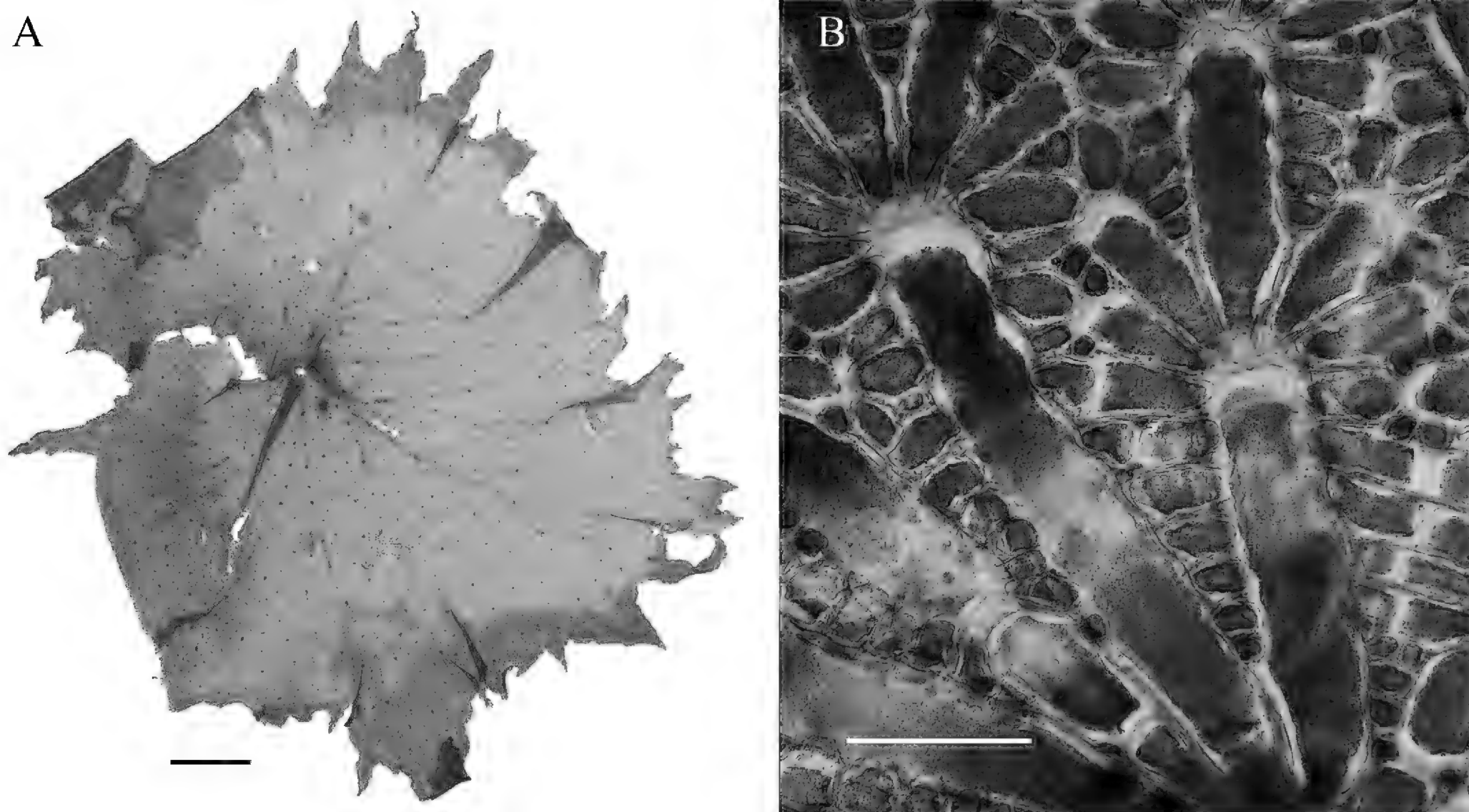


FIGURE 80. *Anadyomene lacerata*. (A) DLB3391, herbarium specimen: Monito Island, 40 m, collected by D. S. Littler and M. M. Littler. Scale bar = 1.0 cm. (B) DLB-8111, photomicrograph: Vieques Island, 49 m, collected by David Anderson, showing arrangement of vein and interstitial cells. Scale bar = 500 μm.

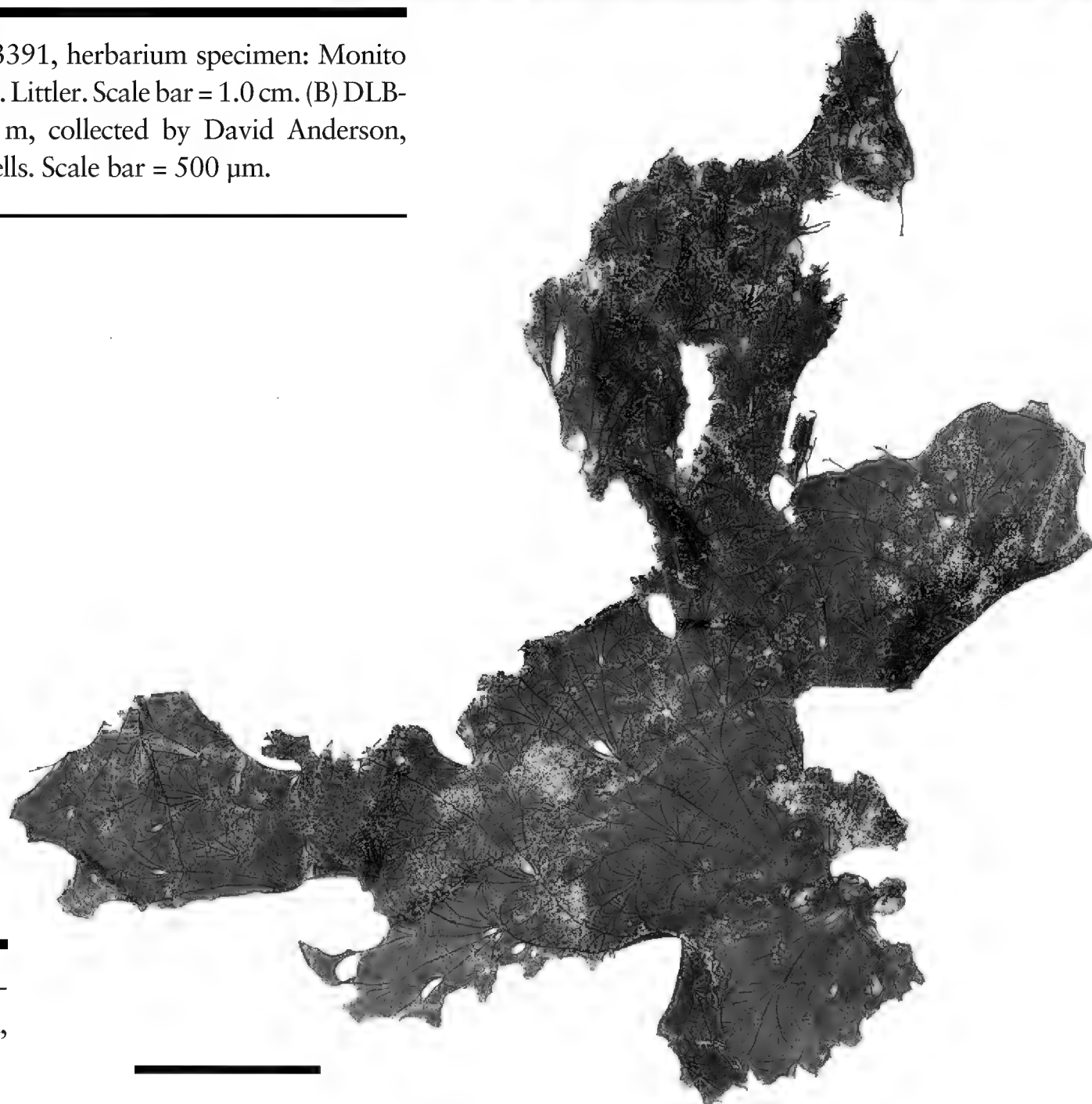


FIGURE 81. *Anadyomene rhizoidifera*. DLB-8468, herbarium specimen: East Mona Island, 46–55 m. Scale bar = 1.0 cm.

Venezuela (Vera et al. 2011). Littler and Littler (1991) discussed overlapping characters in *A. rhizoidifera* and *A. stellata* and concluded that further study was required to determine whether they are actually conspecific. The holotype collection was apparently made of beach cast material, and Alves et al. (2011) did not provide depth information. The Venezuelan report was based on collections from 18 m depth. [Additional illustrations: Alves et al. 2011: figs. 31–42.]

***Anadyomene saldanhae* A. B. Joly et E. C. Oliveira**

FIGURE 82

*Anadyomene saldanhae* A. B. Joly et E. C. Oliveira 1969: 30, figs. 1–3.

*Puerto Rican Records:* Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution:* Belize, Panama, North America, Bermuda, Bahamas, Cuba, Martinique, Netherlands Antilles, Puerto Rico, St. Eustatius, Brazil.

*Type Locality:* Banco Dogareza, off the coast of Victoria, Espírito Santo State, Brazil.

Thalli are either erect, reaching a height of 9.0 cm, or prostrate in low-light habitats. Lacking a well-defined stipe, algae are attached by rhizoids growing from vein cells at the base of the blade. Blades are rigid, fan shaped or irregularly fan shaped. Uniseriate veins are composed of 3 to more than 12 elongate cells, with 4–6 polychotomous branchlets at their apices. Veins lack overlap of adjacent cells. Interstitial cells

are small, elliptical to irregularly shaped, and irregularly arranged. Interstitial cells attach to each other by pointed or forked prongs usually wedged between adjacent cells. The outer blade margin is composed of small spherical cells. Corticating rhizoids are absent. Algae are grass green in color.

*Habitat and Comments:* *Anadyomene saldanhae* is a common member of deepwater turfs in mesophotic coral reef habitats, having been collected from 36 to 100 m in Puerto Rico (Ballantine et al. 2016). Although it is mostly a deepwater species in its Caribbean range, Bucher et al. (1990) reported the alga as shallow as 7.0 m in the Florida Keys. [Additional illustrations: Littler and Littler 1991: figs. 39–43; Alves et al. 2011: figs. 43–49.]

***Anadyomene stellata* (Wulfen) C. Agardh**

FIGURE 83

*Anadyomene stellata* (Wulfen) C. Agardh 1823: 400.

*Basionym:* *Ulva stellata* Wulfen in Jacquin 1787: 351.

*Homotypic Synonyms:* *Anadyomene stellata* var. *luxurians* De Toni 1889: 369; *Anadyomene stellata* var. *floridana* J. E. Gray 1866a: 47.

*Heterotypic Synonym:* *Anadyomene flabellata* J. V. Lamour. 1812: 187.

*Puerto Rican Distribution:* As *Anadyomene stellata*: Almodóvar and Blomquist 1961; Almodóvar 1964a, 1971; Ballantine 1977, 1979; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a; Ballantine et al. 1987; Ballantine and Aponte 2002; Ballantine et al. 2016.

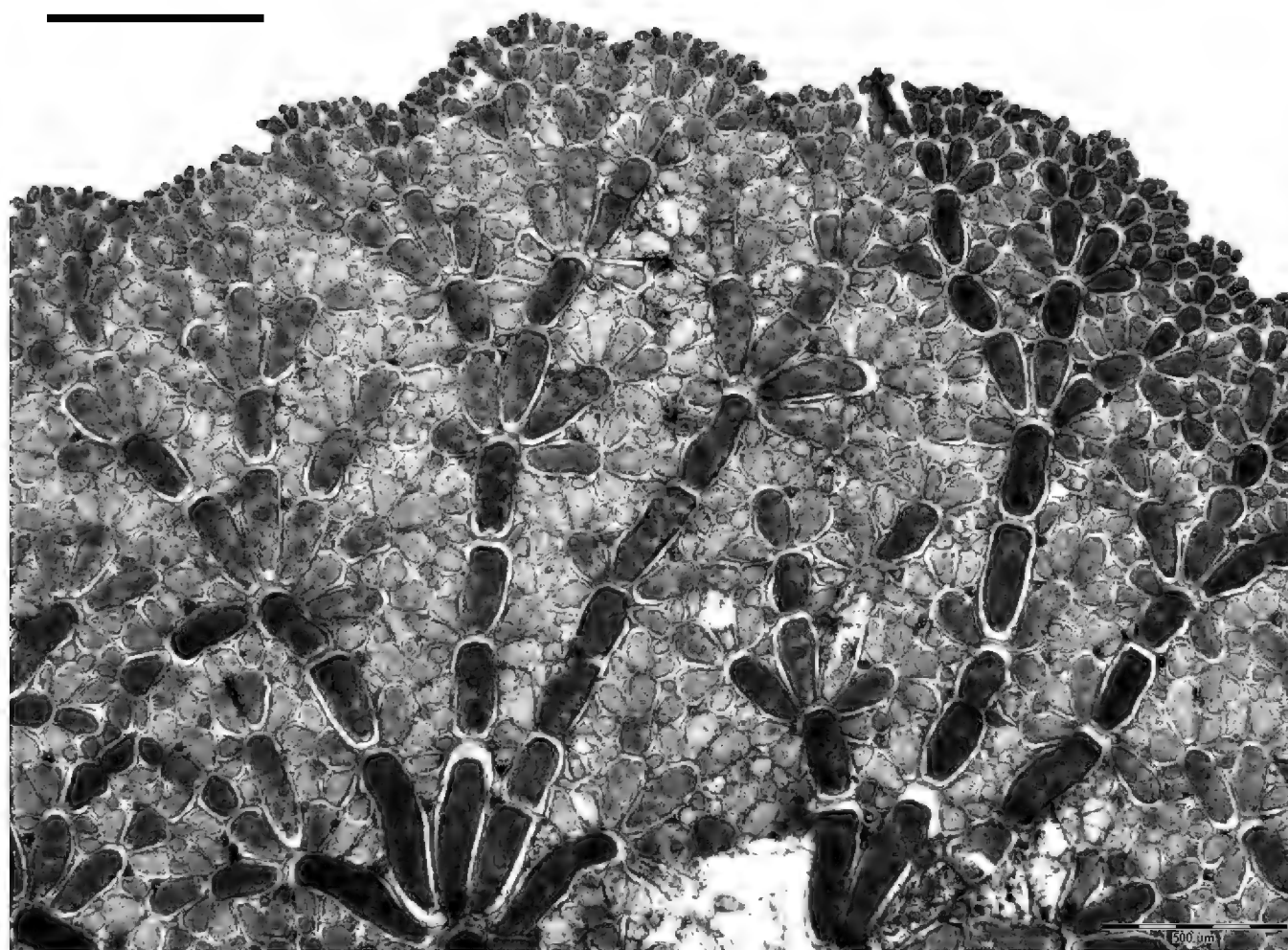


FIGURE 82. *Anadyomene saldanhae*. DLB-3124: Grappler Bank, 100 m. Photomicrograph showing arrangement of vein cells. Scale bar = 500  $\mu$ m.

**Western Atlantic Distribution:** Belize, Costa Rica, Panama, North America, Bahamas, Bermuda, Antigua, Barbados, Barbuda, Cuba, Dominica, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Nevis, Nicaragua, Providencia, Puerto Rico, St. Lucia, St. Eustatius, St. Martin, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Venezuela.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Adriatic Sea.

Occurring singly or, more commonly, in clusters, thalli are anchored by rhizoids loosely entangled to form short stipes in immature individuals, attaching over a broad area in mature thalli. Corticating rhizoids, usually 3–9, are adjacent and parallel to veins. The ruffled blades are crisp and somewhat rigid, measuring 3.0–10 cm in height. The blades are ovate to reniform in shape, 1 cell layer thick and with mostly entire margins. Cells of the blade margins are small and spherical. Blade cells branch in fan-shaped arrangements, forming veins. Uniseriate veins consist of 1–3 cylindrical to clavate cells; branching is polychotomous, with 2–6 branches at segment apices. Vein cells range from 1.8 to 3.0 mm long, 0.25–0.38 mm wide, and have bifurcated bases that straddle apices of proximal segments. The space between veins is filled with oval to elongate interstitial cells. Lateral interstitial cells are H shaped, pinnate, and pectinate. Algae are light yellow green to deep green.

**Habitat and Comments:** Although generally considered to be a shallow-water alga, *Anadyomene stellata* is common in off-shore algal plains and is also known to 100 m in Puerto Rico. The species occurs at a broad range of depths throughout the Caribbean. Littler and Littler (1990: 113) recognized *A. stellata* as a

highly variable species, which included different morphs: “*stellata*” (figs. 48–51), *A. stellata* var. *floridiana* (figs. 52–54), and *A. stellata* var. *luxurians* (figs. 55–56). [Additional illustrations: as *Anadyomene flabellata*, Harvey 1858: pl. 44A; as *Anadyomene stellata*, Vickers 1908: pl. 21; Littler et al. 2008: 192; Braune and Guiry 2011: fig. 7.1.]

### ***Microdictyon* Decne.**

*Microdictyon* Decne. 1841.

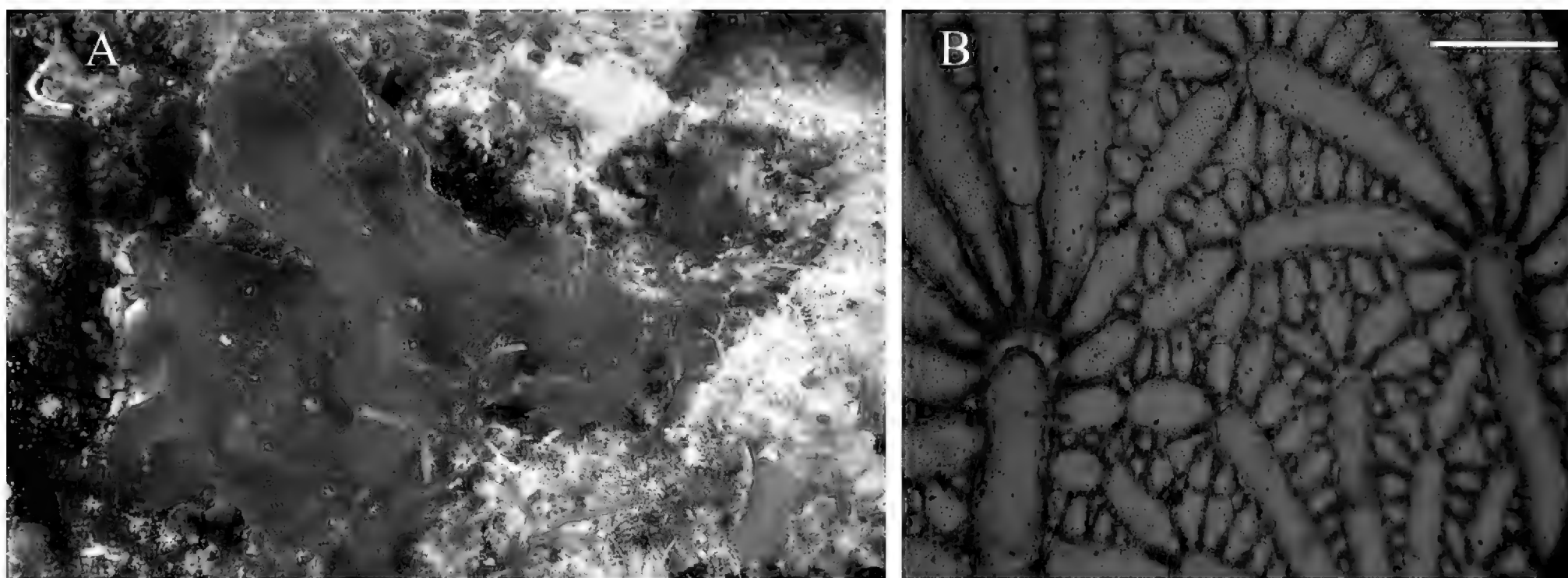
Thalli are membranous and crisp, measuring 2.0–10 cm tall. The base is attached by unicellular, sparingly divided rhizoids extending from the initial cell and larger neighboring cells. The membrane is netlike and composed of monosiphonous branched filaments; branchlet tips attach themselves to subsequent filament cells with a terminal wall thickening. Fifteen *Microdictyon* species are currently recognized; however, Kraft (2000) indicated that, ultimately, as few as four species will be justifiable. One of these species is known in Puerto Rico.

### ***Microdictyon boergesenii* Setchell**

FIGURE 84

*Microdictyon boergesenii* Setchell 1925: 106.

**Puerto Rican Records:** Diaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.



**FIGURE 83.** *Anadyomene stellata*. (A) In situ habit, algal plain, seaward of Media Luna Reef, 17 m. Field = approximately 10 cm. (B) DLBsn: In situ habit, algal plain, seaward of Media Luna Reef, 17 m. Photomicrograph showing arrangement of vein and interstitial cells. Scale bar = 250  $\mu$ m.



*Western Atlantic Distribution:* Belize, Mexico, Panama, North America, Bermuda, Bahamas, Barbados, Cuba, Guadeloupe, Jamaica, Martinique, Puerto Rico, U.S. Virgin Islands, Venezuela, Brazil.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Cruz Bay, St. John Island, U.S. Virgin Islands.

Thalli form delicate meshes, mostly 3.0–6.0 cm across. Algae are composed of primary filaments with unilateral branches, mostly cut off perpendicularly to form a monostromatic, net-like structure with quadrate to irregular-shaped openings, 0.3–0.4 mm in diameter, with outer margins fringed by projecting branchlets. Primary filament cell measures 210–600  $\mu\text{m}$  long and 110–130  $\mu\text{m}$  diam, and secondary filaments measure 145–280  $\mu\text{m}$  long and 70–90  $\mu\text{m}$  diam. Special hapteral cells are not present; branchlets abutting adjacent filaments attach by an apical cell with an annulated adhesion pad at the apex. Filaments lack corticating rhizoids. Thalli are frequently concrescent, and reproduction is unknown. Algae are pale green in color.

*Habitat and Comments:* *Microdictyon boergesenii* is a very common element in the deepwater algal turf community in the Bahamas (Ballantine and Aponte 2003) and in Puerto Rico, where it has been collected to 100 m depth (Ballantine et al.

2016). The species was also reported by Dawes and Mathieson (2008) from shallow-water habitats, 2–10 m, in Florida.

*Microdictyon boergesenii* has been treated as a synonym of *M. umbilicatum* (Vellay) Zanardini 1862 (e.g., Wynne 2017); however, others considered them to be distinct (e.g., Leliaert et al. 2007; Littler and Littler 2000; Dawes and Mathieson 2008; Alves et al. 2011; Ballantine et al. 2016). Setchell (1925) originally felt that *M. umbilicatum* was improperly used with respect to Caribbean plants and erected *M. boergesenii* as a substitute. Although both species have similar apical annulated adhesion pads, the two differ in branching patterns and the presence or absence of apical cell constrictions (Alves et al. 2011). *Microdictyon boergesenii* has unilateral branching and apical cells with constriction, whereas the branching is opposite to polychotomous in *M. umbilicatum* and the apical cells lack constrictions at apex (Alves et al. 2011). [Additional illustrations: Alves et al. 2011: fig. 1A–I; Cormaci et al. 2014: FP297, figs. 4–5.]

#### BOODLEACEAE BØRGESEN

#### *Boodlea* G. Murray et De Toni

*Boodlea* G. Murray et De Toni in Murray 1889.

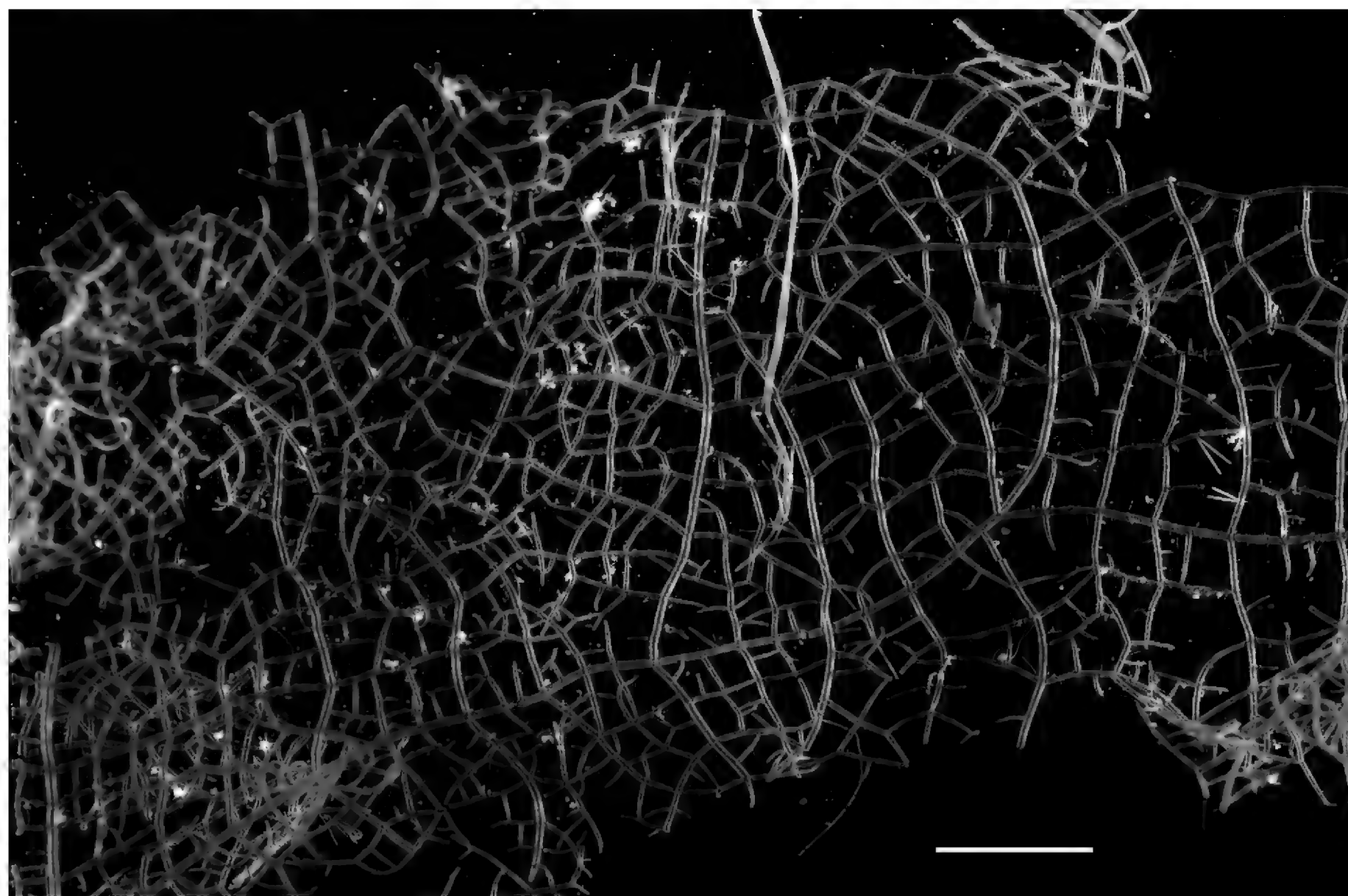


FIGURE 84. *Microdictyon boergesenii*. DLB7422: Edge of insular shelf, La Parguera, 50 m. Scale bar = 2.0 mm.



Thalli are spongy, often conrescent. Filaments arise from the basal attachment, branching freely in all directions. Anastomosing branches commonly attach by tentacular cells at the tips to other

branches with which they come into contact. The result is an often poorly defined three-dimensional shape. There are two species of *Boodlea* in Puerto Rico, out of six species worldwide.

#### KEY TO THE *BOODLEA* SPECIES OF PUERTO RICO

1. Branching irregular throughout ..... *B. composita*  
    Branching often opposite ..... *B. struveoides*

#### ***Boodlea composita* (Harv.) F. Brand**

FIGURE 85

*Boodlea composita* (Harv.) F. Brand 1904: 187, pl. 6: figs. 28–35.

*Basionym*: *Conferva composita* Harv. 1834: 157.

*Puerto Rican Records*: As *Boodlea composita*: Taylor 1960; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution*: Mexico, North America, Bermuda, Barbados, Cuba, Guadeloupe, Martinique, Netherlands Antilles, Puerto Rico, U.S. Virgin Islands, Brazil, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Cap Malheureux, Mauritius.

Thalli are bushy, composed of loosely tangled filaments forming spongy masses, up to 3.0 cm in height. The outer margins often bear short branchlets, and lowermost portions are attached to the substratum by inconspicuous rhizoidal basal

extensions of main filament cells. Cells of the main filaments measure 200–350(–450)  $\mu\text{m}$  diam and up to 20 times the diameter in length. Branched in more than one plane, with branches on the main filaments initially unilateral or opposite and becoming whorled or irregular. Cells of branchlets when first formed measure 70–100(–200)  $\mu\text{m}$  diam and 400–800(–1,600)  $\mu\text{m}$  long and lack basal cross walls that may or may not develop later. Terminal cells of branchlets abutting adjacent filaments attach by a specialized hapteroid cell at the apex. Cells of filaments contain elongate, hexagonal or trapeziform to needle-shaped prismatic crystals (Leliaert and Coppejans 2004: table 1, 2007: table 3). Algae are light grass green in color.

*Habitat and Comments*: *Boodlea composita* occurs to 10 m depth in Puerto Rico. Molecular analyses of *Boodlea composita*, *Phyllocladon anastomosans*, and allied taxa based on rDNA sequences suggest that these taxa are part of a species complex (Leliaert and Coppejans 2007) and should be referred to as morphotypes; the generic and species boundaries remain poorly defined. Leliaert and Coppejans (2007) indicated high phenotypic plasticity and developmental variability among the morphotypes. [Additional

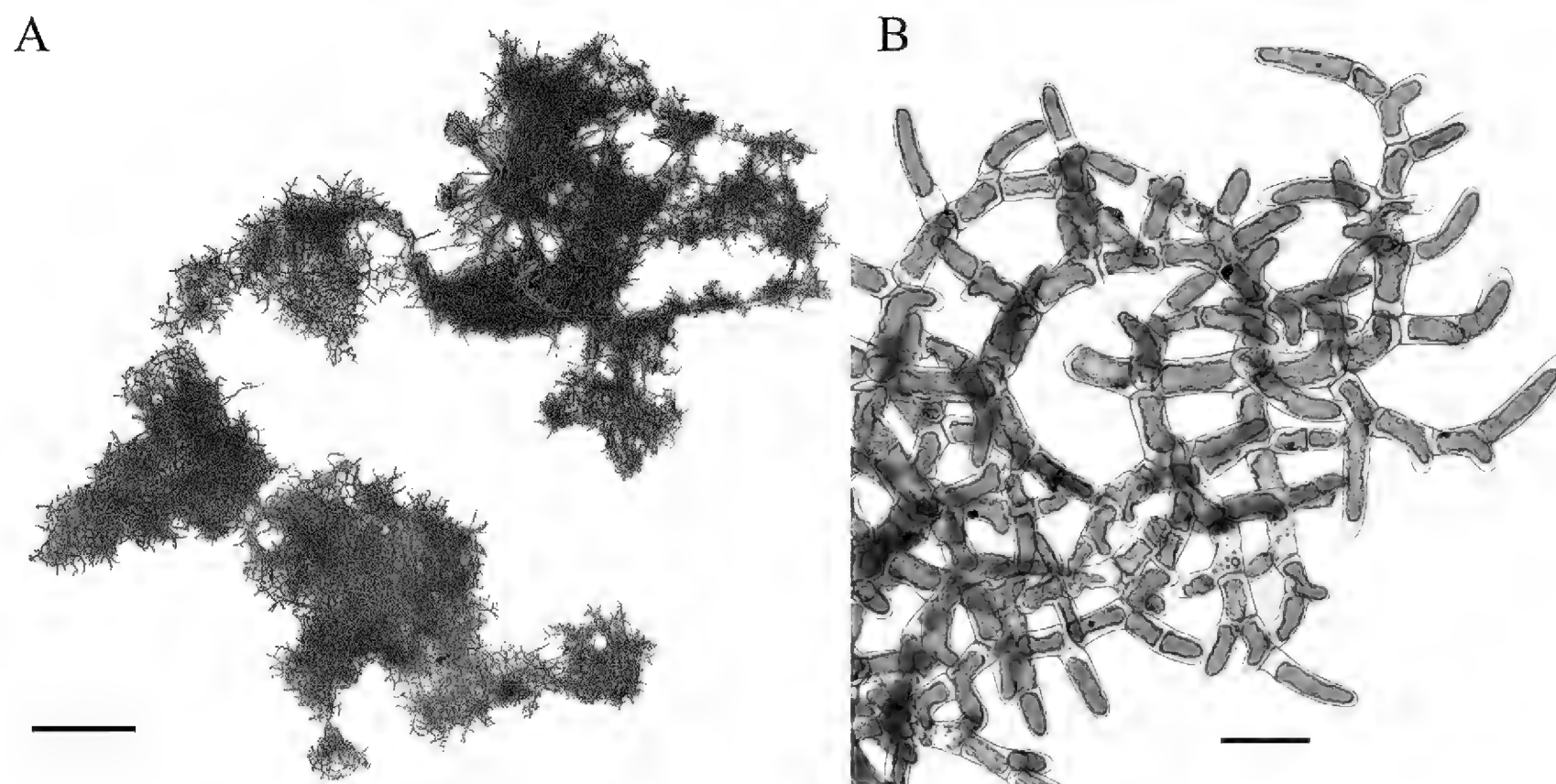


FIGURE 85. *Boodlea composita*. (A) DLB6933: Enrique Reef, La Parguera, epiphytic on *Rhizophora mangle*. Scale bar = 1.0 cm. (B) DLB5029: Enrique Reef, La Parguera, epiphytic on *Rhizophora mangle*. Photomicrograph. Scale bar = 500  $\mu\text{m}$ .

illustrations: Børgesen 1940: fig. 6; Leliaert and Coppejans 2007: figs. 7A–C, 8A–J (lectotype illustrations of *Conferva composita*); Alves et al. 2012a: fig. 1A–X; Huisman 2015: fig. 6A.]

### ***Boodlea struveoides* M. Howe**

*Boodlea struveoides* M. Howe 1918: 496.

*Puerto Rican Records:* Ballantine and Wynne 1986; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Bermuda, Puerto Rico, Trinidad and Tobago.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Harrington Sound, Bermuda.

Thalli occur in spongy masses that are erect or sometimes prostrate, 0.5–7.0 cm in extent. Algae possess firm, arching, tangled filaments that branch in more than one plane with no distinct pattern. Plants are borne on a simple or dichotomously divided stalks, 5.0–30 mm long and up to 2.5 mm diam. Erect thalli are attached below by a small, pad-like holdfast and, if prostrate, also by additional hapteron-like rhizoids. Main filament cells, 200–460 µm diam and 0.8–1.8 mm long, are often oppositely or occasionally irregularly branched, with branchlets 60–80 µm diam and 120–320 µm long. Terminal filament cells are often attached to other filaments by a specialized hapteron-like cell at the apex. Algae are grass green in color.

*Habitat and Comments:* *Boodlea struveoides* occurs in shallow waters on hard substratum to 10 m depths. The type specimen was collected on rocks at an approximate depth of 0.3 m (Howe 1918). [Illustrations: Littler and Littler 2000: 327.]

### ***Cladophoropsis* Børgesen nom. cons.**

*Cladophoropsis* Børgesen 1905, nom. cons.

Thalli are generally caespitose or turf-like, with a basal layer of colorless entangled filaments, attached by multicellular haptera, from which arise erect, crowded filaments, without a distinct axis but abundantly laterally branched. Filaments are uniseriate with multinucleate cells. Filaments possess regularly placed septa; lateral branches arise immediately beneath septa, remaining in open connection with the bearing cell. Chromatophores possess many small pyrenoids. Algae are yellow or bright green in color. *Cladophoropsis* plants bear strong resemblance to *Cladophora* but differ in the lack of septation at the base of young branches. The genus has nine species, two of which are known to Puerto Rico.

*Notes:* Generic limits are complicated by the few morphological characters of *Cladophoropsis*; for example, growth form and branching patterns are environmentally influenced (Leliaert et al. 2003). In a revision of the genus, molecular phylogenetic studies supported the close relationship of *Cladophoropsis* to *Boodlea*, *Phyllodictyon*, *Struveopsis*, *Struvea*, and *Chamaedoris* and concluded the genus should be maintained pending further molecular analyses (Leliaert and Coppejans 2006).

## KEY TO THE *CLADOPHOROPSIS* SPECIES OF PUERTO RICO

1. Filaments 170 to 270 µm in diameter ..... *C. membranacea*  
     Filaments greater than 350 µm in diameter ..... *C. macromeres*

### ***Cladophoropsis macromeres* W. R. Taylor**

*Cladophoropsis macromeres* W. R. Taylor 1928: 64, pl. 4: figs. 15–16.

*Puerto Rican Records:* Diaz-Piferrer 1963; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Belize, Mexico, North America, Bermuda, Barbados, Cuba, Jamaica, Netherlands Antilles, Puerto Rico, Brazil.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Fort Jefferson (Garden Key), Dry Tortugas, Florida, USA.

Thalli are composed of loosely entangled, coarse, cylindrical filaments that form loose mats up to 15 cm in extent and 2.0–10(–15) cm thick. Main filaments measure (280–)350–510 µm diam and 100–5,500 µm long (length to width [L/W] ratio:

~2.3–18). Lateral branches are cut off unilaterally; they measure 210–300 µm diam and are of irregular lengths, up to 5.0 mm long. Apical cells are (140–)280–360(–400) µm diam and up to 22 mm long. Branching is irregular proximally and generally secund distally. Tentacular cells at apices of branchlets attach to other filaments. Chloroplasts, 7.0–10 µm in diam, are polygonal or rounded, forming a parietal reticulum; most have a single large pyrenoid. Crystalline calcium oxalate inclusions, elongate rectangular or trapezoidal to needle shaped and 150 µm long and 1.0–14 µm wide, occur in most cells (Leliaert and Coppejans 2006: figs. 3–4). Algae are bright green in color.

*Habitat and Comments:* In Puerto Rico, *Cladophoropsis macromeres* occurs in protected shallow-water habitats. The species may be unattached, floating or lying on bottom, or entangled with other algae. [Illustrations: Taylor 1960: pl. 2: fig. 2; Leliaert and Coppejans 2006: figs. 18–23.]

***Cladophoropsis membranacea* (Bang ex C. Agardh)  
Børgesen**

FIGURE 86

*Cladophoropsis membranacea* (Bang ex C. Agardh) Børgesen 1905: 289, figs. 8–13.

*Basionym*: *Conferva membranacea* Bang ex C. Agardh 1824: 120–121.

*Puerto Rican Records*: As *Cladophoropsis membranacea*: Almodóvar and Blomquist 1959, 1961; Taylor 1960; Almodóvar 1962, 1964a; Schwartz and Almodóvar 1971; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution*: Costa Rica, Mexico, Panama, North America, Bermuda, Bahamas, Barbados, Cuba, Grenadines, Guadeloupe, Hispaniola, Honduras, Martinique, Netherlands Antilles, Puerto Rico, St. Barthélemy, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: St. Croix, U.S. Virgin Islands.

Thalli are spongy cushions, up to 12 cm wide, or mats up to 50 cm in extent and 2.0–5.0(–10) cm tall, composed of branched, tight or loosely entangled filaments. Algae are attached to the substratum by branched multicellular colorless rhizoids from the proximal end of basal cells or laterally on cells from any part of the thallus. Main filaments are branched to 2–3(–4) orders and measure (90–)170–260(–289)  $\mu\text{m}$  diam and 750–5,000 long. Lateral branches, 100–175  $\mu\text{m}$  diam, are in open connection with main filament cells. Ultimate branch cells, (90–)140–290  $\mu\text{m}$  diam and 100–5,000  $\mu\text{m}$  long, are unilateral or irregularly cut off. Basal filament cells measure (90–)220–260(–280)  $\mu\text{m}$  diam and 250–1,700(–3,000)  $\mu\text{m}$  long. Adjacent cells sometimes anastomose by attachment of tentacular cells, 80–120  $\mu\text{m}$  diam and 180–290  $\mu\text{m}$  long. Chloroplasts, 2.5–7  $\mu\text{m}$  diam with strands up to 20  $\mu\text{m}$  long, are polygonal, elongated to star shaped, and form an open parietal reticulum. Chloroplasts contain a single pyrenoid. Prismatic calcium oxalate crystalline inclusions,

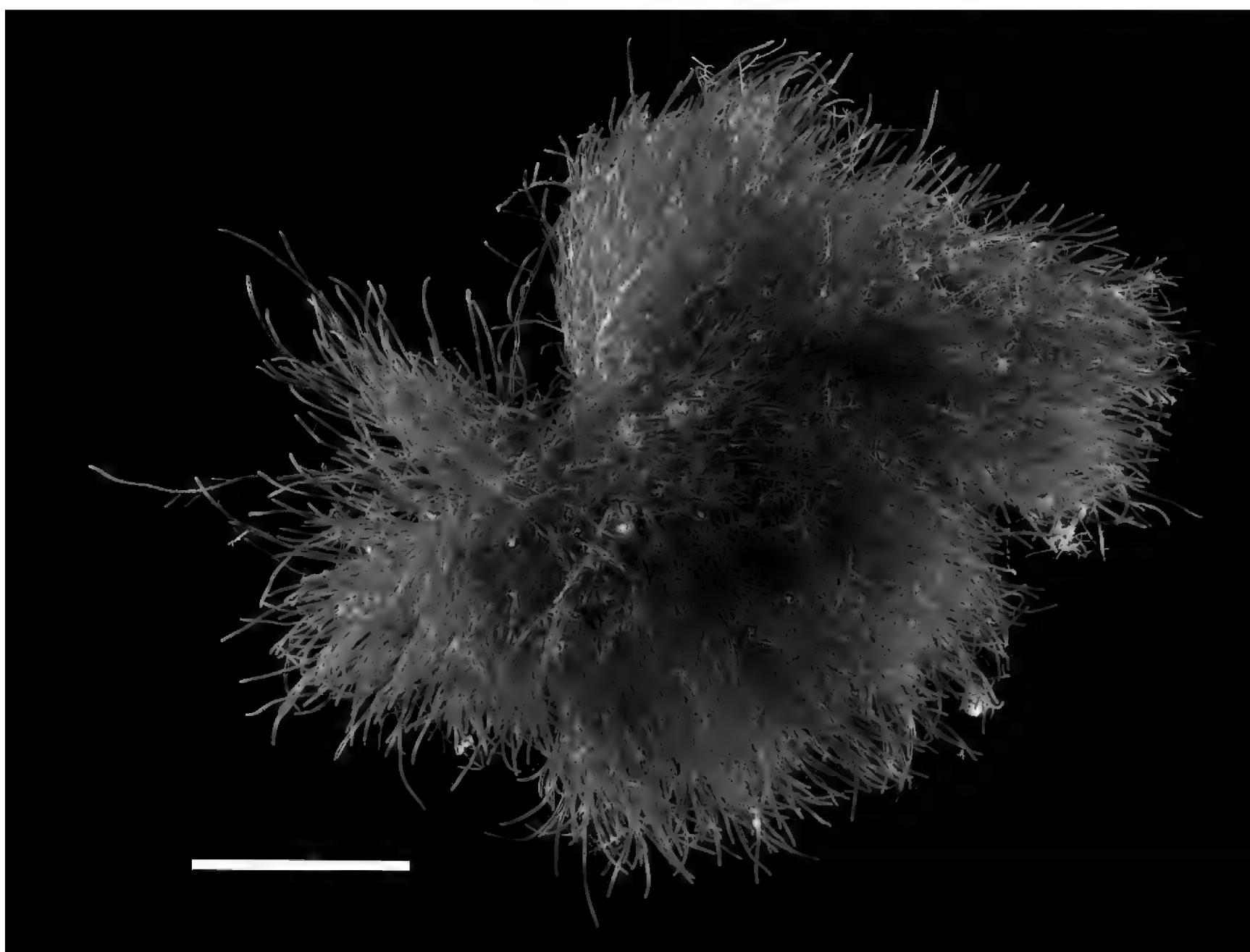


FIGURE 86. *Cladophoropsis membranacea*. Seaward Media Luna Reef, La Parguera, 17 m. Scale bar = 1.0 cm.

60–90 µm long and 1.5–10 µm wide, occur in large numbers in most cells and are highly variable in shape (Leliaert and Coppejans 2006: figs. 7–12).

**Habitat and Comments:** In Puerto Rico, *Cladophoropsis membranacea* commonly occurs as cushions on hard substratum and epiphytically on mangrove roots in the intertidal to shallow water and from 17 to 24 m depths at offshore algal plains. Van der Strate et al. (2002) found that Atlantic “*C. membranacea*” consists of at least of three cryptic species, and their relationship to Indo-Pacific “*C. membranacea*” requires study. *Cladophoropsis membranacea* was shown to have close morphological and molecular affinities with *Boodlea composita* (Leliaert et al. 2007), and phylogenetic analysis of Mediterranean, NE Atlantic, and Caribbean specimens of “*C. membranacea*” revealed them to be on different branches within the *Chamaedoris* clade (Leliaert et al. 2007). [Additional illustrations: Vickers 1908: pl. 17; Børgesen 1913: figs. 28–29; Taylor

1928: pl. 4, fig. 14, 1960: pl. 2: fig. 1, pl. 3: fig. 2; Leliaert and Coppejans 2006: figs. 18–23.]

### ***Phyllodictyon* J. E. Gray**

*Phyllodictyon* J. E. Gray 1866: 69–70.

Arising from simple or branched monosiphonous stalks, thalli produce 1 or more broad netlike blades in one plane. Branching is initially opposite, becoming flabellate by production of additional pairs of opposite branches in the same plane. Blade filaments terminate in tentacular cells that fuse with other branches to form the network. There are nine recognized species of *Phyllodictyon*, of which two are known from Puerto Rico.

**Note:** Kraft and Wynne (1996) utilized the character of segregative cell division that occurs in *Struvea* to separate it from the morphologically similar genus, *Phyllodictyon*, in which parent cells divide by centripetal wall ingrowths.

### KEY TO THE *PHYLLODICTYON* SPECIES OF PUERTO RICO

1. Thalli 3.0–5.0 cm tall; stipe rarely branched, with a reticulate blade, with midrib and 4–8 oppositely paired branches . . . . . *P. anastomosans*
- Thalli 3.0–30 cm tall; stipe commonly with 2–3 branches, each with a reticulate blade with distinct midrib and 8–12 (or more) pairs of branches . . . . . *P. pulcherrimum*

### ***Phyllodictyon anastomosans* (Harv.) Kraft et M. J. Wynne**

FIGURE 87

*Phyllodictyon anastomosans* (Harv.) Kraft et M. J. Wynne 1996: 139.

**Basionym:** *Cladophora anastomosans* Harv. 1859: pl. 101.

**Homotypic Synonym:** *Struvea anastomosans* (Harv.) Picc. et Grunow ex Picc. 1884: 20.

**Heterotypic Synonym:** *Struvea delicatula* Kütz. 1866: 1–2, pl. 2e–g.

**Puerto Rican Records:** As *Phyllodictyon anastomosans*: Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016. As *Struvea anastomosans*: Taylor 1960; Almodóvar and Blomquist 1965; Ballantine 1977; Almodóvar et al. 1979; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987.

**Western Atlantic Distribution:** Belize, Costa Rica, Nicaragua, Panama, North America, Bahamas, Barbados, Cuba, Dominica, Guadeloupe, Jamaica, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Venezuela.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Fremantle, Western Australia.

Thalli are clustered, rarely solitary, reaching 3.0–5.0 cm tall. Filaments of the main axis or stalk measure 200–900 µm diam. Stalks are usually unbranched (rarely branched) and

unsegmented proximally and segmented distally, bearing in a plane 4–6 pairs of opposite branchlet filaments that divide with decreasing regularity to form the network, also in one plane. Ultimate filaments are 100–140 µm diam. Branchlets possess specialized hapteroid cells at apices that attach to adjacent cells. Algae are light to dark green in color.

**Habitat and Comments:** *Phyllodictyon anastomosans* is typically a species of shallow water in Puerto Rico and the Caribbean, where it is found on mangrove prop roots and hard substratum to 1.0 m depth; however, it is also known to 36 m depth in Puerto Rico. In Puerto Rico the netlike blades of *P. anastomosans* can entangle and become attached to each other. Leliaert and Coppejans (2007) referred to *P. anastomosans* as a morphotype in a species complex (see comments under *Boodlea composita* above). [Additional illustrations: as *Struvea delicatula*, Vickers 1908: pl. 19; as *Struvea anastomosans*, Børgesen 1912: fig. 15; Kraft and Wynne 1996: figs. 16–25; Braune and Guiry 2011: fig. 10.1.]

### ***Phyllodictyon pulcherrimum* J. E. Gray**

FIGURE 88

*Phyllodictyon pulcherrimum* J. E. Gray 1866: 70.

**Homotypic Synonym:** *Struvea pulcherrimum* (J. E. Gray) Murray et Boodle 1888: 281.

**Heterotypic Synonyms:** *Struvea ramosa* Dickie 1874b: 316; *Microdictyon curtissiae* W. R. Taylor 1955: 69, text figs. 1–8, pl. 1: fig. 2, pl. 3.



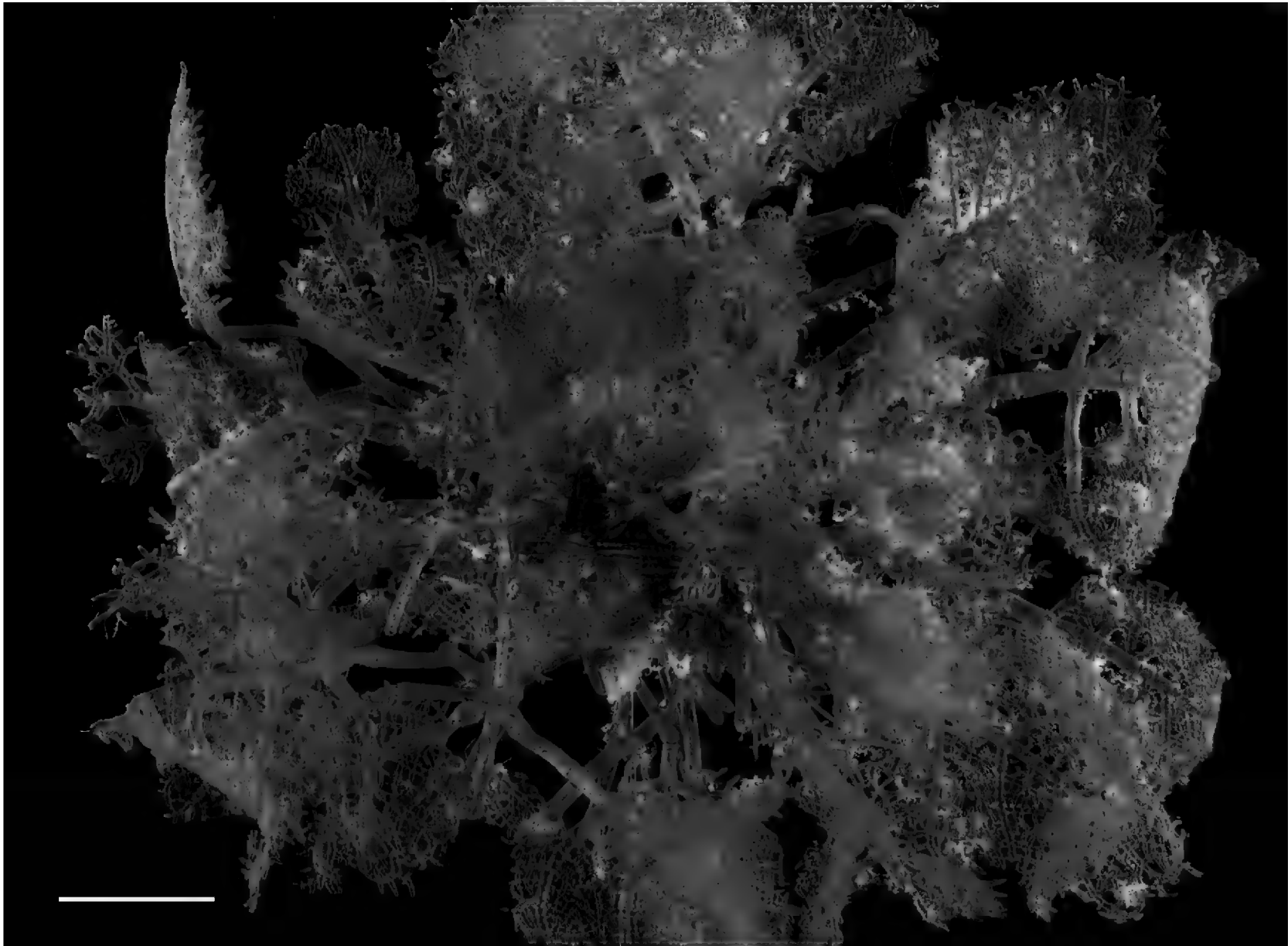


FIGURE 87. *Phyllodictyon anastomosans*. Leeward Enrique Reef, growing on *Rhizophora*. Scale bar = 1.0 cm.

*Puerto Rican Records:* As *Phyllodictyon pulcherrimum*: Ballantine and Aponte 1997a, 2002; Leliaert and Coppejans 2004; Ballantine et al. 2016. As *Struvea ramosa*: Ballantine and Wynne 1986.

*Western Atlantic Distribution:* Costa Rica, Mexico, North America, Bermuda, Barbados, Cuba, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, Venezuela, Brazil.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Gulf of Mexico.

*Phyllodictyon pulcherrimum* is the generitype species. Thalli, to 10 cm tall, are solitary or in clusters of 2–3 branches bearing reticulate blades. They are attached to the substratum by a lobed basal holdfast. The main axial stalk measures 200–1,500  $\mu\text{m}$  diam and possesses 8–12 sets of opposite branches that are repeatedly oppositely rebranched. The meshed blades with distinct midribs reach 30 cm long and 20 cm broad. Specialized hapteral cells at branch apex attach to adjacent cells. Algae are green in color.

*Habitat and Comments:* *Phyllodictyon pulcherrimum* is an exclusively deepwater alga in Puerto Rico, having been reported

to a depth of 70 m (Ballantine et al. 2016). Dawes and Van Breedveld (1969) reported the species from 20 to 80 m in the Gulf of Mexico off the west coast of Florida. The species apparently also occurs in shallow water to 5 m depths in the Florida Keys (Dawes and Mathieson 2008). [Additional illustrations: Kraft and Wynne 1996: figs. 26–28.]

#### ***Struvea* Sond. nom. cons.**

*Struvea* Sond. 1845, nom. cons.

Thalli, 1.0–30 cm tall, are composed of 1 or more blades, each a loosely or tightly woven network of filaments, borne on a simple or rarely branched, aseptate stipe, 1.0–10 cm long. Stipes, 500–2,000  $\mu\text{m}$  diam, are with or without annular constrictions. Blade growth is apical and uniaxial and structurally reinforced by small tentacular cells cut off from adjacent branches. Rhizoids are well developed, branched, and septate where new uprights may develop. Cells are multinucleate and contain multiple discoid chloroplasts, each with a single pyrenoid.



FIGURE 88. *Phyllodictyon pulcherrimum*. DLB8056: Mona Island, 70 m. Scale bar = 5.0 mm.

***Struvea elegans* Børgesen**

FIGURE 89

*Struvea elegans* Børgesen 1912: 264, figs. 13, 14.

*Puerto Rican Records:* Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016,  
*Western Atlantic Distribution:* North America, Bermuda, Cuba, Puerto Rico, St. Eustatius, U.S. Virgin Islands, Brazil.  
*Syntype Localities:* Channel between St. Thomas and St. John; near Thatch Cay, St. Thomas; and off American Hill, north side of St. John, U.S. Virgin Islands [channel between St. Thomas and St. John fide Leliaert and Coppejans (2004: 203)].  
*Lectotype Locality:* Off America Hill, St. Jan, Virgin Islands, Caribbean Sea, fide Schneider and Lane (2007: 129).

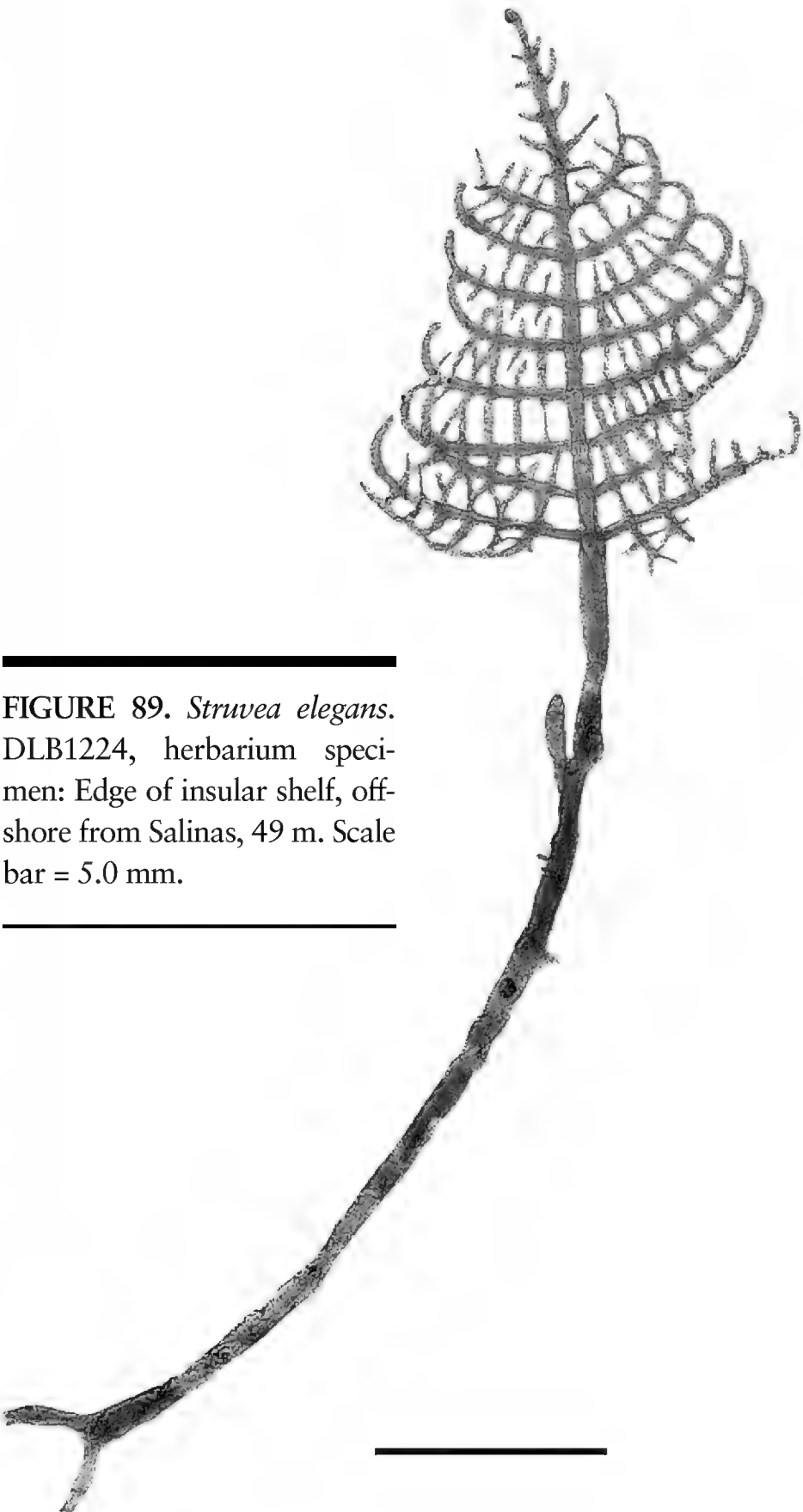


FIGURE 89. *Struvea elegans*. DLB1224, herbarium specimen: Edge of insular shelf, offshore from Salinas, 49 m. Scale bar = 5.0 mm.

Thalli, 1.0–4.0(–12) cm tall, have a creeping base that is attached by branched rhizoids. The lower axial cell is large—2.0–3.0 cm long and 0.8–1.3 mm in diameter—and is slightly annulate proximally. The mesh-like blade when young is regular and symmetrical, 4.0–7.5 mm long and 3.0 cm. broad, in one plane. The blade possesses a pronounced midrib, bearing 14–20 sets of opposite lateral branchlets that are redivided to 2–4 degrees. Cell apices attach to adjacent cells with tentacular projections. Algae are dark green in color.

**Habitat and Comments:** *Struvea elegans* is mostly restricted to deepwater habitats in the western Atlantic. In Puerto Rico, the species is known from 46 to 70 m depths (Ballantine et al. 2016), and in the Florida Keys it is known from 40 to 60 m depths (Leichter et al. 2008). [Additional illustrations: Børgesen 1912: figs. 13–14, 1913: figs. 37, 38a–g; Taylor 1960: pl. 9: figs. 1, 8–9; Schneider and Lane 2007: figs. 2–4.]

## CLADOPHORACEAE W. WILLE

### *Chaetomorpha* Kütz. nom. cons.

*Chaetomorpha* Kütz. 1845, nom. cons.

*Chaetomorpha* consists of uniseriate unbranched filaments that are either unattached without basal cells and free-floating,

loose lying, or entangled or attached by an elongate, thick-walled basal cell and solitary, in clumps or mat forming. The filaments are composed of large, cylindrical to barrel-shaped cells or, rarely, oval cells, and although they are usually not constricted between the cells, some are constricted (Leliaert and Boedeker 2007). Cells are thick walled and multinucleate and as long as broad or up to 10 times longer than wide. Growth is typically through intercalary cell division. Asexual reproduction is by fragmentation. Life histories, where known, consist of isomorphic sporophytic and gametophytic stages. Sexual reproduction is by biflagellate isogametes; in some species gametes are parthenogenetic, repeating the gametophytic life history stage. Currently, 78 species of *Chaetomorpha* are recognized; 6 of these are known from Puerto Rico.

**Notes:** Molecular studies by Boedeker et al. (2016, 2017) revealed separate lineages within *Chaetomorpha*. The generic type, *C. melagonium* (F. Weber et D. Mohr) Kütz. (1845), comprised a monotypic lineage that was distinct from the lineage of other species of “*Chaetomorpha*.” Although this left the species of the latter lineage without a generic name, Boedeker et al. (2016) noted they planned to propose conservation of the name *Chaetomorpha* for those species and will give *C. melagonium* a new generic name.

## KEY TO THE *CHAETOMORPHA* SPECIES OF PUERTO RICO

1. Plants erect, basally attached ..... 2  
Plants flexuous, entangled without specific basal attachment ..... 3
2. Erect filaments broader apically than below ..... *C. clavata*  
Erect filaments of nearly uniform diameter; basal cell elongate ..... *C. antennina*
3. Filaments less than 100 µm diam ..... *C. gracilis*  
Filaments more than 100 µm diam ..... 4
4. Cells mostly isodiametric, filaments to 175 µm diam ..... *C. brachygona*  
Filaments reaching diameters greater than 175 µm ..... 5
5. Filaments stiff and curled, cells to 375 µm diam ..... *C. linum*  
Filaments slightly curved, cells to 568 µm diam ..... *C. vieillardii*

### *Chaetomorpha antennina* (Bory) Kütz.

FIGURE 90

*Chaetomorpha antennina* (Bory) Kütz. 1847: 166.

**Basionym:** *Conferva antennina* Bory 1804: 381.

**Heterotypic Synonym:** *Chaetomorpha media* (C. Agardh) Kütz. 1849: 380.

**Puerto Rican Records:** As *Chaetomorpha media*: Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

**Western Atlantic Distribution:** Costa Rica, Nicaragua, Panama, Mexico, North America, Bermuda, Barbados, Cuba, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Nevis, Puerto Rico, St. Eustatius, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Isla Aves, Venezuela, Uruguay.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Réunion, Indian Ocean (Silva et al. 1996: 759).

Thalli are erect and caespitose, with filaments reaching 7.0–10(–20) cm tall. Algae are attached by distinctive, stout, clavate basal cells measuring 400–425 µm diam distally, 8–50 diameters long and (4–)8–12 times as long as the suprabasal cell. Above the basal cell, filament cells are 450–550 µm diam with cells 2–4 diameters long. Algae are dark green in color.

**Habitat and Comments:** *Chaetomorpha antennina* occurs in dense clusters on wave-exposed intertidal rocks. Børgesen (1940) concluded that *C. antennina* and *C. media* were conspecific, an opinion followed by most (e.g., Guiry and Guiry 2022). Gajaria and Patel (1988) considered them to be separate entities, and Howe (1914) felt that the West Indian *C. antennina* should

be referred to *C. media*. Molecular comparisons of type materials of the Indian Ocean *C. antennina* (type locality: Réunion) and the Caribbean taxa *C. media* (type locality: West Indies) and the currently accepted *C. media* var. *stolonifera* W. R. Taylor (1974; type locality: Dominica) will clarify their taxonomic status and phylogenetic relationships. [Additional illustrations: Vickers 1908: pl. 8; Børgesen 1913, figs. 4–5; Leliaert et al. 2011: figs. 2–5.]

***Chaetomorpha brachygona* Harv.**

FIGURE 91

*Chaetomorpha brachygona* Harv. 1858: 87, pl. 46A: figs. 1–2.

*Puerto Rican Records:* Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Belize, Costa Rica, Panama, Mexico, North America, Bermuda, Bahamas, Antigua, Barbados,

Grenadines, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, U.S. Virgin Islands, Puerto Rico, St. Barthélemy, St. Lucia, Brazil, Uruguay, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Syntype Localities:* Key West, Florida Keys; mouth of the Rio Grande (=Rio Bravo), on border of Texas (USA) and Mexico [Key West, Florida Keys, Monroe County, Florida, fide Blair (1983: 192)].

Unbranched thalli are uniseriate and frequently unattached, free-floating and entangled or in loose mats. Cells of the flexuous filaments are slightly swollen, often of similar length and width, and usually thick walled, 75–175  $\mu\text{m}$  diam and 60–175(–420)  $\mu\text{m}$  long, ranging from 0.75 to 3.0 times as long as broad. Cell inclusions are star-shaped clusters of fine needle-shaped crystals (Leliaert and Coppejans 2004). Algae are yellow green in color.

*Habitat and Comments:* *Chaetomorpha brachygona* occurs in shallow water of sheltered salt marshes, mangroves, and seagrass environments. It is reportedly widespread in distribution

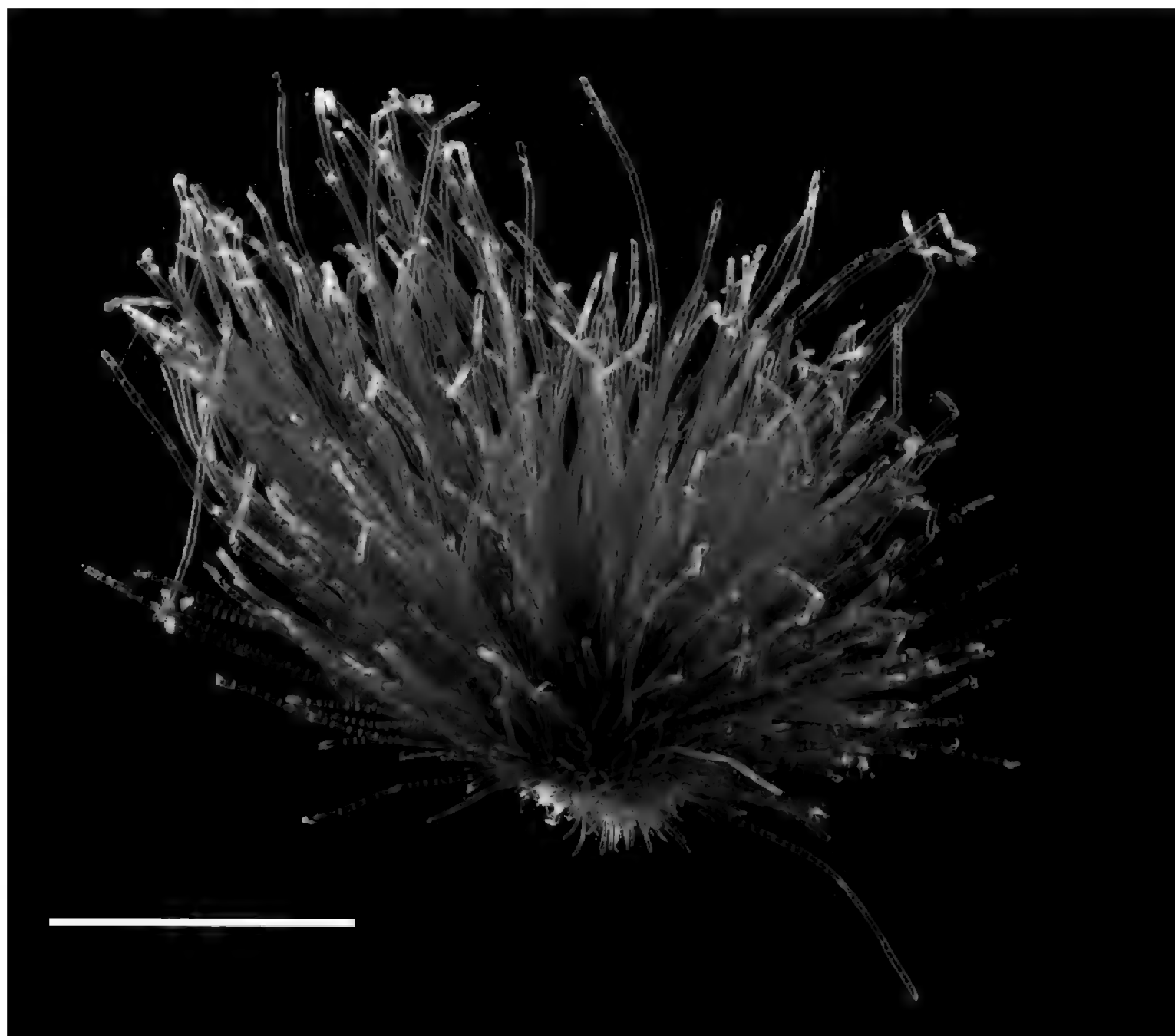


FIGURE 90. *Chaetomorpha antennina*. Intertidal rocks, Ballena Bay, Guánica. Scale bar = 2.0 cm.





FIGURE 91. *Chaetomorpha brachygona*. DLB6502, herbarium specimen: Guajataca, intertidal. Scale bar = 2.0 cm.



FIGURE 92. *Chaetomorpha clavata*. LRA4672, herbarium specimen: Patillas. Scale bar = 2.0 cm.

in the western Atlantic, with records ranging from the subarctic Northumberland Strait, Canada, to the Caribbean (e.g., Dawes and Mathieson 2008; Guiry and Guiry 2022). [Additional illustrations: Taylor 1960: pl. 2: fig. 9; Littler et al. 2008: 193.]

### ***Chaetomorpha clavata* Kütz.**

FIGURE 92

*Chaetomorpha clavata* Kütz. 1847: 166.

*Heterotypic Synonym:* *Conferva clavata* C. Agardh 1824: 99, nom. illeg. [non *Conferva clavata* Roth 1797: 160].

*Puerto Rican Records:* Almodóvar and Blomquist 1961; Almodóvar 1962; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* North America, Bahamas, Barbados, Cuba, Hispaniola, Jamaica, Puerto Rico, St. Barthélemy, St. Eustatius, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* “In mari Indiae Occidentalis” (Agardh 1824: 99); West Indies.

Thalli composed of tufted filaments, up to 30 cm in length, and attached to hard substrata. Thin-walled filament cells are 500–750 µm diam and 1,500–3,000 µm long (about 3–4 times longer than broad) proximally and gradually increasing to 1,050 µm diam or more distally. Lower cells are subcylindrical to cask shaped, and upper cells are moniliform, becoming submoniliform distally.

*Habitat and Comments:* *Chaetomorpha clavata* is apparently rare in Puerto Rico. Kützting (1847) based the taxon on *Conferva clavata* C. Agardh (1824); however, since the intended basionym is an illegitimate name, Silva et al. (1996) treated *Chaetomorpha clavata* as a *nomen nudum* (see also Wynne 1998). [Additional illustrations: Schnetter 1978: pl. 7I–L.]

### ***Chaetomorpha gracilis* Kütz.**

*Chaetomorpha gracilis* Kütz. 1845: 203.

*Puerto Rican Records:* Ballantine et al. 1987; Ballantine and Aponte 1997a.

*Western Atlantic Distribution:* Costa Rica, Panama, North America, Bermuda, Barbados, Cuba, Guadeloupe, Hispaniola, Jamaica, Netherlands Antilles, Puerto Rico, St. Eustatius,

Grenadines, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Trieste, Gulf of Trieste, northeast Italy (Coppjans et al. 2001).

Thalli are composed of entangled, cylindrical filaments, (32–)40–80(–120)  $\mu\text{m}$  diam and 15(–200) cm long. Algae are unattached and free-floating or are attached by a few rhizoidal projections from the basal cell. Filaments are cylindrical, and cells above the basal cells are (40–)80–240  $\mu\text{m}$  long (about 1–2 times as long as broad); the basal cells are 125–360  $\mu\text{m}$  long. Cells of unattached filaments can be longer than those of attached thalli. Algae are yellow green in color.

*Habitat and Comments:* *Chaetomorpha gracilis* occurs in the intertidal, on mangroves, or is free-floating. [Illustration: Littler et al. 2008: 194.]

### ***Chaetomorpha linum* (Müller) Kütz.**

FIGURE 93

*Chaetomorpha linum* (O. F. Müll.) Kütz. 1845: 204.

*Basionym:* *Conferva linum* O. F. Müll. 1778: 7.

*Puerto Rican Records:* As *Chaetomorpha linum*: Almodóvar 1964a; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Panama, Costa Rica, North America, Bermuda, Bahamas, Barbados, Cuba, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, St. Barthélemy, St. Kitts, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Argentina.

*World Distribution:* See Guiry and Guiry (2022).

*Syntype Locality:* Nakskov and Rødby, Denmark [Nakskov Fjord, Lolland (municipality), Region Sjælland, west coast of island of Lolland, Denmark, fide Lipkin and Silva (2002)].

Thalli are mostly unattached and loosely entangled in large accumulations. Filaments are stiff and curled, and cells measure (100–)150–375(–450)  $\mu\text{m}$  diam and (50–)450–1,055(–2,250)  $\mu\text{m}$  long (0.5–3[–5] times as long as broad). Cells are thin walled, slightly swollen, and slightly constricted at cross walls. Algae are light green to dark green in color.

*Habitat and Comments:* *Chaetomorpha linum* is entangled, often with other algae and seagrasses, or may be free-floating or lying on the bottom in small to large masses. Generally, it is found in protected shallow-water habitats, including salt marshes and among mangrove roots. [Additional illustrations: Blair 1983: figs. 1, 2a; Littler et al. 2008: 195; Braune and Guiry 2011: fig. 8.1.]

### ***Chaetomorpha vieillardii* (Kütz.) M. J. Wynne**

FIGURE 94

*Chaetomorpha vieillardii* (Kütz.) M. J. Wynne 2011b: 112, figs. 1, 2a,b.

*Basionym:* *Bangia vieillardii* Kütz. 1863: 10.

*Misapplied Name:* *Chaetomorpha crassa* (C. Agardh) Kütz. 1845: 204 [non *Chaetomorpha crassa* (C. Agardh) Kütz. 1845: 204; =*C. aerea* (Dillwyn) Kütz. 1849].

*Puerto Rican Records:* As *Chaetomorpha crassa*: Almodóvar and Blomquist 1965; Almodóvar et al. 1979; Ballantine and Wynne 1986; Ballantine and Aponte 1997a.

*Western Atlantic Distribution:* Costa Rica, North America, Bermuda, Cuba, Puerto Rico, St. Barthélemy, U.S. Virgin Islands, Brazil.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* New Caledonia (Millar and Prud'homme van Reine 2005).

Thalli are uniseriate, unbranched filaments that are slightly curved and loosely entangled. Cells of the filaments are large, coarse, and slightly constricted at septations, measuring 450–700(–900)  $\mu\text{m}$  diam and 450–1,100(–1,800)  $\mu\text{m}$  long (1–2 times as long as broad), with cell walls 10–14  $\mu\text{m}$  thick.

*Habitat and Comments:* *Chaetomorpha vieillardii* is generally found in shallow water, sometimes entangled with other algae. [Additional illustrations: Wynne 2011b: figs. 1–2.]

### **Excluded Taxon**

*Chaetomorpha crassa* (C. Agardh) Kütz. 1845: 204.

Wynne (2011b) reported that the name *Chaetomorpha crassa* has been misapplied to Caribbean material.

### ***Cladophora* Kütz. nom. cons.**

*Cladophora* Kütz. 1843, nom. cons.

Thalli are filamentous, uniseriate, and sparingly to highly dichotomously or secundly branched. Filaments with multinucleate cells are attached or unattached. When attached, attachment is by rhizoids issued from proximal cells. Chromatophores are parietal or reticulate, with many pyrenoids. *Cladophora* is a freshwater and marine genus with 195 species and 25 infraspecific taxa currently recognized worldwide. Nine of these species occur in Puerto Rico.

*Notes:* Hoek (1982: 30) asserted that *Cladophora* is a “rather heterogeneous assemblage of species,” and Taylor (1960) has pointed out that only a few species in the geographical western Atlantic region are distinctive, and others had inadequate descriptions, making accurate determinations for some *Cladophora* species difficult. This situation is quickly obvious to any student of the flora attempting identification of species of *Cladophora*.



FIGURE 93. *Chaetomorpha linum*. DLB5067, herbarium specimen: Magueyes Island, collected by X. Connelly. Scale bar = 2.0 cm.

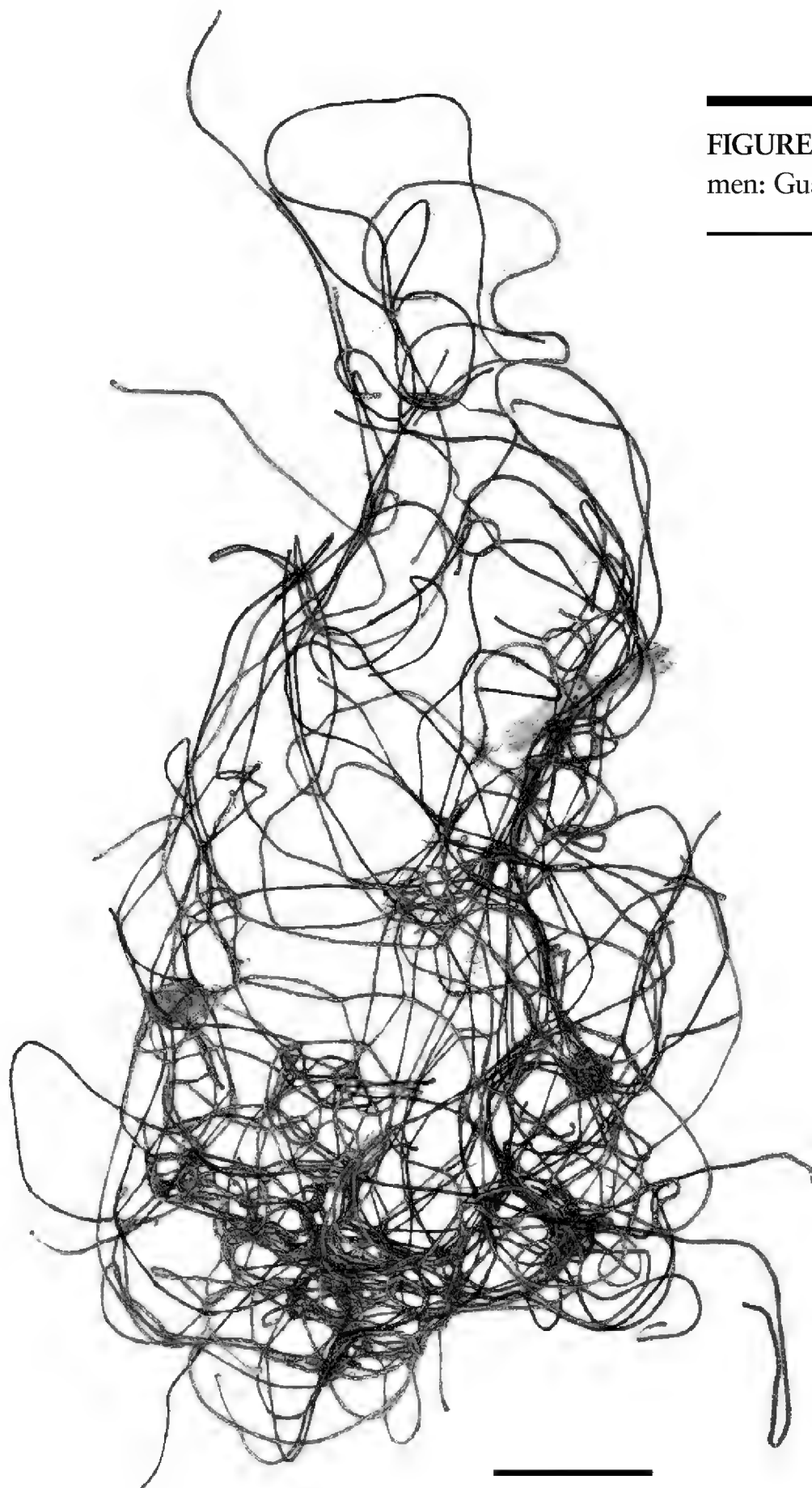


FIGURE 94. *Chaetomorpha vieillardii*. DLB1517, herbarium specimen: Guayacan Island, 1.0 m. Scale bar = 2.0 cm.

KEY TO THE CLADOPHORA/WILLEELLA SPECIES OF PUERTO RICO

- 1. Algae mostly prostrate ..... *C. coelothrix*  
Algae without a prostrate filament system ..... 2
- 2. Thalli possessing microscopically visible endophytic fungal spores within cell walls ..... *C. fuliginosa*  
Thalli not possessing endophytic fungal spores ..... 3
- 3. Algae with notably fasciculate branchlets ..... 4  
Algae without fasciculate branching ..... 5
- 4. Plants coarse; dark green, becoming blackish on drying; rhizoids annulate ..... *C. prolifera*  
Thalli soft; bright green, not blackening on drying ..... *C. vagabunda*
- 5. Algae occur in mat-like growth ..... 6  
Algae not occurring in mats ..... 8
- 6. Main branch diameter less than 50  $\mu$ m diam ..... *C. dalmatica*  
Main branch diameter greater than 50  $\mu$ m diam ..... 7
- 7. Branch tips frequently strongly incurved, main axis 50–70  $\mu$ m diam ..... *C. socialis*  
Branch tips mostly straight, main axis 42–140  $\mu$ m diam ..... *C. submarina*



8. Main axes greater than 100  $\mu\text{m}$  in diameter ..... *C. laetevirens*  
 Main axes less than 100  $\mu\text{m}$  in diameter ..... 9
9. Algae occur in dense clumps, 10 cm tall; cell walls thick, annulate; branch apices falcate ..... *C. conferta*  
 Thalli occur in small tufts, 30 cm high; cell walls not annulate; branch apices not falcate ..... *W. brachyclados*

### ***Cladophora* sect. *Aegagropila* (Kütz.) Hansg.**

*Cladophora* sect. *Aegagropila* (Kütz.) Hansg. 1886: 85.

*Basionym*: *Aegagropila* Kütz. 1843: 272.

### ***Cladophora fuliginosa* Kütz.**

FIGURE 95

*Cladophora fuliginosa* Kütz. 1849: 415.

*Heterotypic Synonyms*: *Conserva catenata* L. 1753: 1166.

*Puerto Rican Records*: As *Cladophora fuliginosa*: Diaz-Piferrer 1963; Ballantine 1977; Almodóvar and Ballantine 1983.  
 As *Cladophora catenata*: Almodóvar and Blomquist 1965; Almodóvar et al. 1979; Hoek 1982; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution*: Belize, Panama, Mexico, North America, Bahamas, Bermuda, Antigua, Cayman Islands, Cuba, Dominica, Guadeloupe, Hispaniola, Honduras, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, St.

Lucia, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Havana, Cuba.

Thalli are composed of firm, stiff, curved, and intertwined cylindrical filaments, dichotomously or alternately branched, that form tufts 3.0–15 cm high. Cells of main axes measure 150–160(–450)  $\mu\text{m}$  diam (L/W ratio: 5–10). Filament branches bear short, blunt branchlets in second series. Cells contain chloroplasts with pyrenoids, and the cell walls are generally infested by an endophytic fungus, *Blodgettomyces borneti* (E. P. Wright) Feldmann, very evident microscopically by its large conidia/spores (Johnson and Sparrow 1961). Algae are bright green to brownish green in color.

*Habitat and Comments*: *Cladophora fuliginosa* occurs in shallow water in both wave-exposed and protected environments as well as to 55 m depth. Hoek (1969) noted *C. fuliginosa* does not occur in the Mediterranean, and its reported distribution is the western Atlantic, western Pacific, Australia and New Zealand, and Oman (Indian Ocean; Guiry and Guiry 2022). The nomenclature and taxonomic status need clarification (see Delnatte and Wynne 2016). [Additional illustration: Taylor 1928: pl. 4: fig. 5.]

### ***Cladophora* sect. *Glomeratae* Kütz.**

*Cladophora* sect. *Glomeratae* Kütz. 1843: 91.

### ***Cladophora dalmatica* Kütz.**

*Cladophora dalmatica* Kütz. 1843: 268.

*Heterotypic Synonyms*: *Cladophora luteola* Harv. 1858: 8.

*Puerto Rican Records*: Hoek 1982; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution*: Massachusetts, Connecticut, Rhode Island, Sargasso Sea, Virginia, North Carolina, Bermuda, Florida, Bahamas, Florida Keys, Mississippi, Texas, Gulf of Mexico, Caribbean Mexico, Jamaica, Haiti, Sargasso Sea, Grand Cayman Island, Puerto Rico, Guadeloupe, Panama, Curaçao, Colombia, Venezuela, Guyana, and Brazil.

*Other Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Split, Split-Dalmatia (county), Croatia, eastern Adriatic Sea.

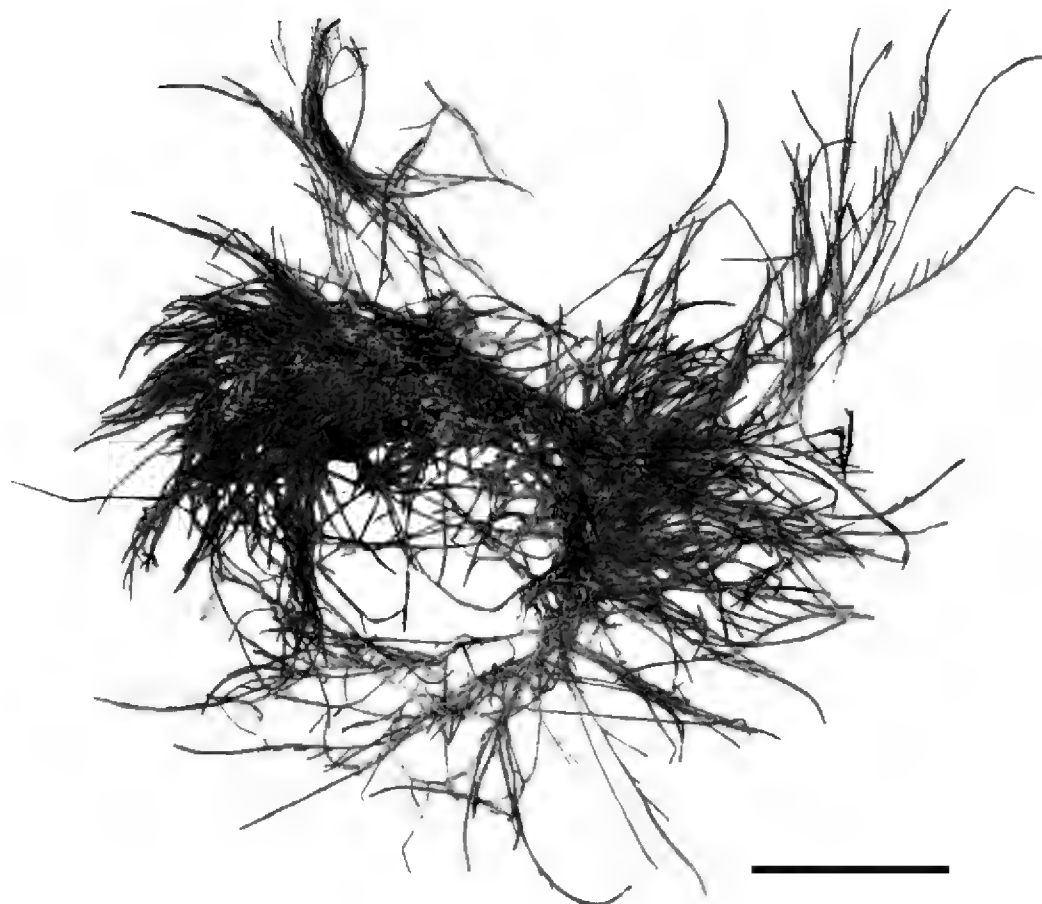


FIGURE 95. *Cladophora fuliginosa*. DLBsn, herbarium specimen: Algal plain, seaward Media Luna Reef, 17 m. Scale bar = 2.0 cm.

Thalli form spongy tufts of branched cylindrical filaments, 0.5–2.0(–5) cm tall in exposed habitats and up to 20 cm tall in protected habitats. Algae are attached by rhizoids developed from basal and lowermost cells. Individuals often become entangled and form spreading mats on hard substrata. Main axes are pseudodichotomously and pseudotrichotomously branched, up to 5 orders. Upper branching is falcate, with ultimate branches that are more or less straight or slightly curved. Cells of the main axes are 25–40(–65)  $\mu\text{m}$  diam (L/W ratio: 2.5–14), and basal cells of filaments are partly fused. Cells of ultimate branches are 14–42  $\mu\text{m}$  diam (L/W ratio: 3–10). Apical cells are 14–32  $\mu\text{m}$  diam (L/W ratio: 2.0–13). Cell walls of main axis cells are 1.0–4.0  $\mu\text{m}$  thick and in ultimate branches 0.5–1.0  $\mu\text{m}$  thick. Algae are light to dark green in color.

**Habitat and Comments:** *Cladophora dalmatica* can be common on rocks and boulders in sandy areas, occurring in exposed and protected habitats from the lower intertidal to shallow waters and in tide pools and down to 60–65 m deep in Curaçao (Hoek 1978). The species is occasionally epiphytic. [Illustrations: as *Cladophora dalmatica*, Kützinger 1854: pl. 13: fig. 1; Vickers 1908: pl. 14b; Cormaci et al. 2014: pl. 72: figs. 2–3; as *Cladophora luteola*, Hoek 1982: pl. 30: figs. 295–312.]

### ***Cladophora laetevirens* (Dillwyn) Kütz.**

*Cladophora laetevirens* (Dillwyn) Kütz. 1843: 263.

**Basionym:** *Conferva laetevirens* Dillwyn 1805: pl. 48.

**Misapplied Name:** *Cladophora utriculosa* Kütz. 1843: 269

**Puerto Rican Records:** As *Cladophora utriculosa*: Taylor 1960. As *Cladophora laetevirens*: Hoek 1982; Ballantine and Aponte 1997a, 2002.

**Western Atlantic Distribution:** Belize, Panama, North America, Bermuda, Barbados, Cuba, Martinique, Netherlands Antilles, Puerto Rico, St. Eustatius, U.S. Virgin Islands, Brazil, Colombia, Argentina, Uruguay.

**Other Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Swansea, Glamorgan (county), Wales, UK.

Thalli are spongy tufts, 0.5–3.0 cm tall, in exposed habitats and elongated tufts, 5.0–20 cm high, in protected habitats. Branching is pseudodichotomous and pseudotrichotomous, often densely. Attachment is by rhizoids from a basal cell and lowermost cells that become partially coalesced. Branches are unilateral and nearly straight to incurved, 2(–3) per node, and mostly acropetally branched. Filament cells of the main axes are 53–205  $\mu\text{m}$  diam (L/W ratio: 3–11). Cells of ultimate branches are 45–105  $\mu\text{m}$  diam (L/W ratio: 2–9). Apical cells are 37–105(–150)  $\mu\text{m}$  diam (L/W ratio: 2–11) and have rounded apices. Cell walls in distal portions are 1.0–2.0  $\mu\text{m}$  thick and up to 20  $\mu\text{m}$  thick proximally. Chloroplasts are parietal, with portions containing bilenticular pyrenoids, and form dense networks in low-light conditions and a more open network in higher-light regimes. Algae are light to dark green in color.

**Habitat and Comments:** *Cladophora laetevirens* grows on hard substratum, rocks or coral fragments, or epiphytically. It occurs in wave-exposed habitats intertidally and in shallow protected waters to 2.0 m depths. Leliaert and Boedeker (in Brodie et al. 2007) noted *C. laetevirens* may be conspecific with *C. hutchinsiae* (Dillwyn) Kütz. (1845). [Illustrations: Hoek 1982: pl. 23: figs. 238–261, pl. 24: figs. 250–255, pl. 25: figs. 256–261; Hoek and Chihara 2000: figs. 82A–F, 83G–I, 84K–L, 85M–O; Littler et al. 2008: 198 (a copy of the type illustration); Cormaci et al. 2014: pl. 75: figs. 3–4; as *Conferva laetevirens*, Dillwyn 1805: pl. 48.]

### ***Cladophora vagabunda* (L.) C. Hoek**

FIGURE 96

*Cladophora vagabunda* (L.) C. Hoek 1963: 144, pl. 33: figs. 434, 436–439, pl. 36: figs. 470–490, pl. 37: figs. 491–503, pl. 39: figs. 505–514.

**Basionym:** *Conferva vagabunda* L. 1753: 1167.

**Heterotypic Synonyms:** *Cladophora fascicularis* (Mertens ex C. Agardh) Kütz. 1843: 268; *Cladophora pulverulenta* (K. Mert.) Phinney 1945: 445.

**Puerto Rican Records:** As *Cladophora vagabunda*: Hoek 1963; Ballantine and Aponte 1997a, 2002. As *Cladophora fascicularis*: Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar 1964a, 1964b; Almodóvar and Ballantine 1983. As *Cladophora pulverulenta*: Almodóvar and Ballantine 1983.

**Western Atlantic Distribution:** Belize, Mexico, North America, Bermuda, Bahamas, Barbados, Cayman Islands, Cuba, Grenadines, Guadeloupe, Hispaniola, Honduras, Jamaica, Puerto Rico, St. Barthélemy, St. Kitts, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Uruguay, Venezuela.

**Other Distribution:** See Guiry and Guiry (2022).

**Lectotype Locality:** In salt marsh; Selsey, Manhood Peninsula, West Sussex (county), England (Hoek 1963: 19, 144; Lipkin and Silva 2002).

Thalli are composed of pseudodichotomously branched filaments, with 2(–3) branches per node, that form spongy tufts. Plants are 30(–46) cm tall and attached to hard substratum or are unattached. Cells of the main axes are 120–250(–350)  $\mu\text{m}$  diam (L/W ratio: 2.5–7.0). Ultimate branches are in fasciculate groups 1.5–3.0 mm long and often strongly recurved, with cells (24–)70–90(–160)  $\mu\text{m}$  diam (L/W ratio: 2.5–8). Proximal cells of main axes are 2.5–9.5 times longer than wide and generally partly fused. Thalli occurring in protected habitats are less acropetal to irregular in organization. Algae are pale green to grass green, sometimes gray green, in color.

**Habitat and Comments:** Although *Cladophora vagabunda* occurs attached in tide pools and on rocks and other hard substratum in exposed locations, it can also be loose-lying or free-floating mats in partial to very protected habitats, such as lagoons and salt marshes. [Additional illustrations: as *Cladophora fascicularis*, Vickers 1908: pl. 13; as *Cladophora vagabunda*, Hoek 1982: pl.



FIGURE 96. *Cladophora vagabunda*. DLB2183, herbarium specimen: Yabucoa Bay, intertidal. Scale bar = 2.0 cm.

26: figs. 264–273 (note that figs. 265–273 are from Puerto Rico specimens), pl. 27: figs. 274–281, pl. 28: figs. 282–288, pl. 29: figs. 289–294; Cormaci et al. 2014: pl. 79: figs. 1–3.]

### ***Cladophora* sect. *Longiarticulatae* Hamel**

*Cladophora* sect. *Longiarticulatae* Hamel 1924: 170.

### ***Cladophora conferta* P. Crouan et H. Crouan**

*Cladophora conferta* P. Crouan et H. Crouan in Schramm and Mazé 1865: 37.

*Heterotypic Synonym:* *Cladophora uncinata* Børgesen 1913: 20, figs. 9–10.

*Puerto Rican Records:* Hoek 1982; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Bermuda, Cuba, Guadeloupe, Jamaica, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Uruguay, Venezuela.

*Other Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Guadeloupe, West Indies, Caribbean Sea.

Thalli form dense clumps or tufts 1.0–5.0(–10) cm high, composed of coarse filaments. Attachment is by spreading rhizoids with annulate/undulating walls, produced from the basal cell and the lower ends of proximal branches. The main axes are not distinct and bear numerous pseudodichotomous and pseudotrictotomous divisions that branch up to 4 orders in an acropetal pattern. Filaments of the main axes are of cylindrical cells 32–95  $\mu\text{m}$  diam (L/W ratio: 2–8). Proximal cells are irregularly cylindrical, thick walled, (12–)25–67  $\mu\text{m}$  diam (L/W ratio: 2–8) and become irregularly annulate. Ultimate branches are secund and sometimes hooked, with cells 27–53  $\mu\text{m}$  diam (L/W ratio: 3.5–7.5). Apical cells are cylindrical or sometimes tapering, 25–45  $\mu\text{m}$  diam (L/W ratio: 2–9), and with rounded apices. Chloroplasts are in parietal overlapping layers or in a parietal reticulum. Algae are dark green in color.

*Habitat and comments:* *Cladophora conferta* is found on hard substratum, usually in protected habitats but also in moderately exposed, shallow-water embayments. [Illustrations: as *C. uncinata*, Børgesen 1913: figs. 9–10; as *C. conferta*, Hoek 1982: pl. 33: figs. 332–334, pl. 34: figs. 335–345, pl. 35: figs. 350–354; Alves et al. 2012b: fig. 5A–K.]

### ***Cladophora* sect. *Repentes* Kütz.**

*Cladophora* sect. *Repentes* Kütz. 1843: 416.

### ***Cladophora coelothrix* Kütz.**

*Cladophora coelothrix* Kütz. 1843: 272.

*Heterotypic Synonym:* *Cladophora repens* Harv. 1849: pl. 236.

*Puerto Rican Records:* As *Cladophora coelothrix*: Hoek 1982; Ballantine and Aponte 1997a; Ballantine et al. 2016. As *Cladophora repens*: Almodóvar and Ballantine 1983.

*Western Atlantic Distribution:* Costa Rica, Mexico, Panama, North America, Bermuda, Bahamas, Cuba, Grenadines, Guadeloupe, Jamaica, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, Brazil, Venezuela, Argentina.

*Other Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Golf von Genua [Livorno, Italy, fide Womersley (1984)].

Thalli form cushion-like turfs of compact mats or loose-lying mats, composed of densely or loosely interwoven filaments, reaching 2.0–5.0 cm tall. Algae are attached by branched basal rhizoids from proximal ends of basal cells or by rhizoids produced by basal or distal ends of lowermost branches. Main axial filament cells are 60–220 µm diam (L/W ratio: 5.0–20); proximal cells of main axes measure 55–235 µm diam. Distal branch cells are 55–140 µm diam (L/W ratio: [3.5–]5–16). Apical cells are 55–140 µm diam (L/W ratio: [2.5–]7–20), with rounded tips. Cell walls in apical portions are about 1.0–5.0 µm thick and 4.0–10(–20) µm thick proximally. Algae are dark green to blackish green in color.

*Habitat and Comments:* *Cladophora coelothrix* is common in mangrove lagoons and wave-exposed habitats. The species is also known to 82 m depths in Puerto Rico (Ballantine et al. 2016) and in the Bahamas from 76 to 82 m depths (Norris and Olsen 1991; Ballantine and Aponte 2003). [Illustrations: Hoek 1982: pl. 2: figs. 11–17, pl. 3: figs. 18–22, pl. 4: figs. 23–29; Alves et al. 2012b, fig. 4A–J; Cormaci et al. 2014: pl. 82: figs. 1–2.]

### ***Cladophora socialis* Kütz.**

*Cladophora socialis* Kütz. 1849: 416.

*Misapplied Name:* *Cladophora crispula* Vickers 1905: 56.

*Puerto Rican Records:* As *Cladophora crispula*: Almodóvar and Blomquist 1965; Almodóvar et al. 1979; Almodóvar and Ballantine 1983. As *Cladophora socialis*: Hoek 1982; Ballantine and Aponte 2002.

*Western Atlantic Distribution:* Costa Rica, Panama, North America, Bermuda, Barbados, Bahamas, Guadeloupe, Hispaniola, Jamaica, Netherlands Antilles, Puerto Rico, U.S. Virgin Islands, Brazil.

*Other Distribution:* See Guiry and Guiry (2022).

*Type Locality:* “Ad litora insulae O’Taiti” (Kützting 1849: 416); in littoral, Tahiti.

Thalli form either irregular, spongy clumps or mats, 2.0–5.0 cm tall. Individual thalli possess filaments interwoven with other algae or are unattached and loose-lying, entangled masses on bottom or free-floating. Branching is distinctly to vaguely acropetal (sometimes irregular). Main axes are spirally pseudodichotomously to pseudotrichotomously branched, with branches terminating in strongly incurved tips. Main axial cells are 45–80 µm diam (L/W ratio: [2–]4–20 diameters long). Ultimate branches measure 23–54 µm diam (L/W ratio: 4–17). Apical cells are 23–54 µm diam (L/W ratio: 7–18). Cell are long,

usually much longer than broad. Cell walls in ultimate branches are less than 1.0 µm thick and up to 2.0–4.0 µm thick in main axes. Algae are light green to dull dark green in color.

*Habitat and Comments:* *Cladophora socialis* occurs on wave-exposed sites in tufts or mats as well as loose patches in mangrove and seagrass environments. Sometimes it grows with *C. coelothrix*. A specimen identified as “*C. crispula*” by Blomquist (DUKE) from Guajataca, Puerto Rico, was properly referred to *C. socialis* (Hoek 1982: 57). Other Puerto Rican specimens identified as “*C. crispula*” should be critically compared to this species. *Cladophora socialis* is also recorded in the Sargasso Sea (Woelkerling 1975) and is probably more widespread in distribution than indicated by current Caribbean records. [Illustrations: as *Aegagophila socialis*, Kützting 1854: pl. 71, fig. 1; as *Cladophora socialis*, Hoek 1982: pl. 5: figs. 30–40; Cormaci et al. 2014: pl. 82: fig. 3.]

### ***Cladophora* sect. *Rugulose* Sakai**

*Cladophora* sect. *Rugulose* Sakai 1964: 67.

### ***Cladophora prolifera* (Roth) Kütz.**

*Cladophora prolifera* (Roth) Kütz. 1843: 271

*Basionym:* *Conferva prolifera* Roth 1797: 182.

*Puerto Rican Records:* Hoek 1982; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Belize, Costa Rica, North America, Bermuda, Barbados, Cuba, Guadeloupe, Martinique, Puerto Rico, Trinidad and Tobago, Brazil, Colombia, Venezuela.

*Other Distribution:* See Guiry and Guiry (2022).

*Type Locality:* “In mare Corsicam” (Roth 1797: 183). The type is apparently lost (Womersley 1984); a neotype was designated by Hoek (1963: 208).

*Neotype Locality:* Miramare, near Trieste, Gulf of Trieste, Adriatic Sea, NE Italy.

Thalli form densely fasciculate, coarse tufts 2.0–10(–25) cm tall, attached by long rhizoids, 40–100 µm diam, growing downwardly from lower axial cells. Indistinct main axes branch dichotomously to trichotomously or pseudotetrachotomously. Cells of the main axes are elongate, measuring 240–345 µm diam (L/W ratio: 4.5–16) proximally; often with annular constrictions in the older, larger cells. More distal cells are 95–240 µm diam (L/W ratio: 1–4), and ultimate branch cells are 95–240 µm diam (L/W ratio: 2.5–7). Apical cells are 95–240 (L/W ratio: 2.0–5.5). Cell walls are thick, 2.0–10 µm thick in ultimate branches and 15–40 µm thick in lowermost portions of main axes. Algae are usually dark green (often blackish when dried) in color.

*Habitat and Comments:* *Cladophora prolifera* is typically found in the lower intertidal, attached to rocks. [Illustrations: Taylor 1960: pl. 3: fig. 5; Schnetter 1978: pl. 8A,B; Hoek 1982: pl. 32: figs. 318–327; Cormaci et al. 2014: pl. 83: figs. 2–4.]



**Cladophora sect. Xanthochlora C. Hoek**

*Cladophora* sect. *Xanthochlora* C. Hoek 1982: 183.

*Xanthochlora* is a monotypic taxonomic section (*secto*) based on *Cladophora submarina*.

**Cladophora submarina P. Crouan et H. Crouan**

*Cladophora submarina* P. Crouan et H. Crouan in Schramm et Mazé 1865: 38.

*Heterotypic Synonyms*: *Cladophora howei* Collins 1909b: 18; *Cladophora luteola* P. Crouan et H. Crouan in Mazé et Schramm 1878: 65, nom. illeg. [non *C. luteola* Harv. 1858: 81; =*C. dalmatica* Kütz. 1843: 268].

*Puerto Rican Records*: As *Cladophora submarina*: Hoek 1982; Ballantine and Aponte 2002. As *Cladophora luteola* sensu Taylor 1960 [non *Cladophora luteola*]: Diaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a.

*Western Atlantic Distribution*: Mexico, North America, Bermuda, Bahamas, Cuba, Guadeloupe, Hispaniola, Martinique, Netherlands Antilles, Puerto Rico, Turks and Caicos, Venezuela.

*Type Locality*: La Moule, Anse de Grouyé, Guadeloupe.

Thalli form dense cushions or extensive mats, 0.5–3.0 cm broad and up to 0.7 cm high, or extensive mats of looser filaments, 1.0–3.0 cm tall, and attached by extensive basal rhizoids developed from basal and suprabasal cells. Filaments of the main axes produce several primary lateral branches, mostly proximally, which in turn develop numerous shorter secondary branchlets irregularly. Cells of the main axes are 42–140 µm diam, and basal cells are 45–200 µm diam (L/W ratio: 3–13). Ultimate branch cells are 36–88 µm diam (L/W ratio: 5–12). Apical cells are cylindrical to slightly tapered, 30–80 µm diam (L/W ratio: 5–24), with obtuse apices. Chloroplasts are in complete or incomplete parietal networks. Cell walls in ultimate branches are less than 1.0 to 1.5 µm thick and in the main axes are up to 3.0 µm thick and about 10 µm thick in basal cells. Algae are yellow green in color.

*Habitat and Comments*: *Cladophora submarina* occurs in habitats constantly exposed to wave action on hard substratum, such as rocks or limestone platforms, and adjacent upper intertidal tide pools. [Illustrations: Hoek 1982: pl. 37: figs. 366–393.]

**Excluded Taxon**

*Cladophora crispula* Vickers 1905: 56.

Puerto Rican records of *Cladophora crispula* were based on the original report of *Cladophora crispula* from Luquillo by Almodóvar and Blomquist (1965). Hoek (1982) subsequently identified Blomquist's specimen as *Cladophora socialis*.

*Cladophora lehmanniana* (Lindenberg) Kütz. 1843: 268.

*Basionym*: *Conferva lehmanniana* Lindenberg 1840: 179 [type locality: Helgoland, Germany].

The only Puerto Rican report of the species from Puerto Rico was in Taylor (1960) as *Cladophora utriculosa*. Some Caribbean specimens identified as “*C. utriculosa*” were referred to other species by Hoek (1982); for example, those he examined from Bermuda and Bahamas were *C. liebetruthii* Grunov. Although Hoek (1982) stated that *C. lehmanniana* is limited to eastern Atlantic coasts of Europe, others since then continue to recognize its presence in the western Atlantic (e.g., Suárez et al. 2015; Wynne 2017). Leliaert and Boedeker (in Brodie et al. 2007) suggested *C. lehmanniana* and *C. hutchinsiae* (Dillwyn) Kütz. could be conspecific.

**Pseudorhizoclonium C. Boed.**

*Pseudorhizoclonium* C. Boed. in Boedeker et al. 2016.

Thalli are composed of filaments, 30–100 µm diam; filaments are either unattached or attached by secondary rhizoids or by a basal cell. Filaments may have sharp-angled bends, often with a short continuation of the cell below the bend. Cells of filaments are short in length and usually have a thick cell wall, greater than 10 µm thick. Cells typically contain (20–)30–40 nuclei per cell. Ten *Pseudorhizoclonium* species are recognized; one of these occurs in Puerto Rico.

*Notes*: *Pseudorhizoclonium* is genetically distinct from the morphologically similar *Rhizoclonium* on the basis of rDNA sequence analysis (Boedeker et al. 2016). The genus is apparently restricted to the tropics, occurring in mangroves, lagoons, and the high intertidal, and appears to be well adapted to brackish waters and changing salinities.

**KEY TO THE RHIZOCLONIUM/PSEUDORHIZOCLONIUM SPECIES OF PUERTO RICO**

1. Cells 40–100 µm diam ..... *P. africanum*  
Cells less than 30 µm diam ..... *R. riparium*

***Pseudorhizoclonium africanum* (Kütz.) C. Boed.**

*Pseudorhizoclonium africanum* (Kütz.) C. Boed. in Boedeker et al. 2016: 922, fig. 8.

*Basionym:* *Rhizoclonium africanum* Kütz. 1853: 21.

*Heterotypic Synonym:* *Rhizoclonium hookeri* Kütz. 1849: 383.

*Puerto Rican Records:* As *Rhizoclonium africanum*: Ballantine and Aponte 1997a, 2002. As *Rhizoclonium hookeri*: Almodóvar and Biebl 1962; Almodóvar et al. 1979; Almodóvar and Ballantine 1983.

*Western Atlantic Distribution:* Panama, Mexico, North America, Bermuda, Bahamas, Cuba, Guadeloupe, Jamaica, Martinique, Puerto Rico, Venezuela, Brazil.

*World Distribution:* See Guiry and Guiry (2022)

*Type Locality:* “Senegambien” [Senegal or Gambia, Africa, fide Index Nominum Algarum (2022)].

*Pseudorhizoclonium africanum* is the generitype. Thalli are composed of stiff uniseriate filaments that are rarely branched. The filaments are sometimes forked with sharp-angled bends or “knees” (sensu Boedeker et al. 2016: fig. 8F), forming a short lateral branch. Cells of the filaments measure 40–80(–100) µm diam (L/W ratio: 2–4), with cell walls (4.0–)10 µm thick.

*Habitat and Comments:* *Pseudorhizoclonium africanum* occurs in tide pools with reduced salinities and grows on marsh plants and mangrove roots or is found unattached in seagrass beds. The plants are usually unattached and entangled or grow epiphytically on mangrove roots. The species has also reported been reported in fresh water in the mainland United States (Smith 1950, as *R. hookeri*) and the Great Lakes (Prescott 1962). [Illustrations: Boedeker et al. 2016: fig. 8A–F.]

***Rhizoclonium* Kütz.**

*Rhizoclonium* Kütz. 1843.

Thalli are composed of uniseriate unbranched to few-branched filaments, often with short lateral rhizoidal branches. Initially basally attached, algae become free and unattached. Cells are cylindrical, typically less than 100 µm diam, and not constricted at septa. Cells are multinucleate and possess thin walls, 1.0–2.0(–4.0) µm. Chromatophores are reticulate and parietal with pyrenoids. *Rhizoclonium* comprises a single species in Puerto Rico. Thirty-nine species of the genus are recognized worldwide.

***Rhizoclonium riparium* (Roth) Harv.**

*Rhizoclonium riparium* (Roth) Harv. 1849: 238, pl. 238.

*Basionym:* *Conferva riparia* Roth 1806: 216.

*Heterotypic Synonyms:* *Rhizoclonium riparium* (Roth) Harv. var. *implexum* (Dillwyn) Rosenv. 1893: 915; *Rhizoclonium implexum* (Dillwyn) Kütz. 1845: 206; *Rhizoclonium kernerii* Stockm. 1890: 582.

*Puerto Rican Records:* As *Rhizoclonium riparium*: Almodóvar and Blomquist 1959; Ballantine and Aponte 1997a. As *R. riparium* var. *implexum*: Ballantine and Aponte 2002. As *Rhizoclonium implexum*: Hinds and Ballantine 1987. As *Rhizoclonium kernerii*: Almodóvar and Blomquist 1965; Ballantine 1977; Almodóvar et al. 1979; Almodóvar and Ballantine 1983.

*Western Atlantic Distribution:* Belize, Costa Rica, Panama, Mexico, North America, Bermuda, Bahamas, Cuba, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Uruguay, Venezuela, Argentina.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Norderney, East Frisian Islands, Germany, North Sea.

Thalli are flaccid, of soft texture, occurring as scattered filaments or dense mats of straight or curved entangled filaments. Thalli are usually unattached. Cells are cylindrical, variable in diameter, 20–39 µm diam and 1–2 diameters long. Apical cells are terete to swollen. Algae are pale, yellowish green to bright or dark green in color.

*Habitat and Comments:* *Rhizoclonium riparium* occurs in shallow-water lagoons, salt marshes, and tide pools, entangled with other algae or forming free-floating mats on the surface or bottom or on hard substratum such as pilings. [Illustrations: Littler et al. 2008: 204; Cormaci et al. 2014: pl. 85: fig. 14.]

***Willeella* Børgesen**

*Willeella* Børgesen 1930.

Thalli are composed of branched, uniseriate filaments, attached by branching basal holdfasts or unattached as aegagropiloid tufts. Main axis or primary laterals are typically lined with short, tapering branchlets, conical apical cells, and up to 6 laterals per cell. Cells of filaments are multinucleate and contain a parietal reticulate chloroplast. Cell divisions are mainly intercalary. Cells of the main axes measure 56–175 µm diam, and apical cells are 24–45 µm diam. Algae are dark to medium green.

*Notes:* The genus was found to form a distinct lineage in phylogenetic reconstructions based on rDNA sequences and was recently emended by Boedeker (in Boedeker et al. 2016), who noted morphological characters alone are not diagnostic.

Two species of *Willeella* are recognized worldwide, with one species known in Puerto Rico. The Puerto Rican “*Willeella*” species cannot be morphologically separated from *Cladophora*.

***Willeella brachyclados* (Mont.) M. J. Wynne**

*Willeella brachyclados* (Mont.) M. J. Wynne 2016: 1.

*Basionym:* *Conferva brachyclados* Mont. 1837: 349 [non *Conferva brachyclados* (Kütz.) P. Crouan et H. Crouan]. (Kütz.) P. Crouan et H. Crouan].

*Heterotypic Synonyms:* *Cladophora montagneana* Kütz. 1847: 166; *Conferva delicatula* Mont. 1850: 302; *Cladophora delicatula* (Mont.) Mont. 1856: 458.

*Puerto Rican Records:* As *Cladophora montagneana*: Hoek, 1982; Ballantine and Aponte 1997a, 2002. As *Cladophora delicatula*: Taylor 1960; Almodóvar and Ballantine 1983.

*Western Atlantic Distribution:* Belize, Mexico, Panama, North America, Bermuda, Barbados, Cuba, Guadeloupe, Hispaniola, Jamaica, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, Brazil, Guyana, Brazil, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Havana, Cuba.

Thalli are loosely branched, not opposite as is characteristic of the genus, with delicate hairlike tufts to a height of 30 cm. Growth is chiefly by intercalary division, and branching is sparsely pseudodichotomous, with ultimate branchlets often in short secund series, attached by basal rhizoids. Cells of filaments are typically cylindrical, with cell walls 4.0–7.0  $\mu\text{m}$  thick in main axes and 1.0–3.0  $\mu\text{m}$  thick in ultimate branchlets. Main axial cells are 40–55(–135)  $\mu\text{m}$  diam (L/W ratio: 0.8–4.0). Ultimate branchlet cells are (13–)20–30  $\mu\text{m}$  diam (L/W ratio: 1–4), and apical cells are 13–30(–40)  $\mu\text{m}$  diam (L/W ratio: 1.5–5.0).

*Habitat and Comments:* *Willeella brachyclados* is generally found among seagrasses in protected, shallow-water habitats. *Willeella* was once considered congeneric with the morphologically similar *Cladophora*, with its generitype, *W. ordinata* Børgesen (1930), placed in *Cladophora*. sect. *Willeella* (Børgesen) Hoek (1982), Boedeker et al. (2016) more recently reinstated the genus primarily on the basis of its molecular distinction. [Illustrations: as *C. montagneana*, Hoek 1982: pl. 16: figs. 145–160, pl. 17: figs. 161–173; as *W. brachyclados*, Alves et al. 2012b: fig. 10A–J.]

## SIPHONOCADACEAE F. SCHMITZ

### *Boergesenia* J. Feldmann

*Boergesenia* J. Feldmann 1938.

Thalli are coenocytic, unbranched pyriform or clavate vesicles characterized by their annulate basal regions, attached by basal rhizoids. Thalli grow as solitary individuals or form rosette-like clusters. Until the genus was recently discovered in the western Atlantic (Ballantine et al. 2009, 2011b), it had been known only in the Indian and Pacific Oceans. Of the three species of *Boergesenia* currently recognized, two are known from Puerto Rico.

## KEY TO THE *BOERGESENIA* SPECIES OF PUERTO RICO

1. Vesicles 10–20 mm in height and to 2.6 mm in breadth ..... *B. parvula*  
     Vesicles much taller, to 6.5 cm in height and to 13 mm in breadth ..... *B. forbesii*

### *Boergesenia forbesii* (Harv.) J. Feldmann

FIGURE 97

*Boergesenia forbesii* (Harv.) J. Feldmann 1938: 1503.

*Basionym:* *Valonia forbesii* Harv. 1860: 333.

*Puerto Rican Records:* As *Boergesenia forbesii*: Ballantine et al. 2009, 2011b.

*Western Atlantic Distribution:* Puerto Rico.

*World Distribution:* See Guiry and Guiry (2022).

*Syntype Localities:* Loo Choo Islands (also Ceylon) [Ryukyu Islands (=Ryūkyū-shotō, Nansei-shotō), Okinawa Prefecture, SW Japan, and Sri Lanka fide Silva et al. (1996)].

*Lectotype Locality:* Type [specimen] from Ryukyu-retto, Japan (Lipkin and Silva 2002: 57).

*Boergesenia forbesii* is the generitype species. Puerto Rican plants grow in small clusters of up to 15 conspicuous vesicles. The vesicles are frequently arched, reaching 6.5 cm in height.

The vesicles are narrow near their base to 0.7 mm diam and expanded above, to 13 mm. Vesicles are normally inconspicuously annulate at their bases although occasionally smooth. Vesicles produce abundant rhizoids from their lower stipes. The rhizoids form a conspicuous, expanded, and highly entangled mat. The rhizoidal mat frequently traps sediment, and on close inspection, young vesicles are abundantly produced from the rhizoids. At the lower surface of the mat, rhizoids give rise to terminal digitate attachments.

*Habitat and Comments:* In Puerto Rico, the species is known only from the Condado Lagoon (San Juan), where it was collected in shallow water, 0.2–0.5 m depth. Despite the substantial geographical separation between Puerto Rico and the Pacific in addition to size discrepancies, preliminary genetic analysis of 18s rDNA sequences revealed a close relationship with Japanese specimens (Ballantine et al. 2011b). *Boergesenia forbesii* is possibly an introduced species to Puerto Rico. [Additional illustrations: as *Valonia forbesii*, Yamada 1934: figs. 1–2; as *Boergesenia forbesii*, Ballantine et al. 2011b: figs. 7–10.]

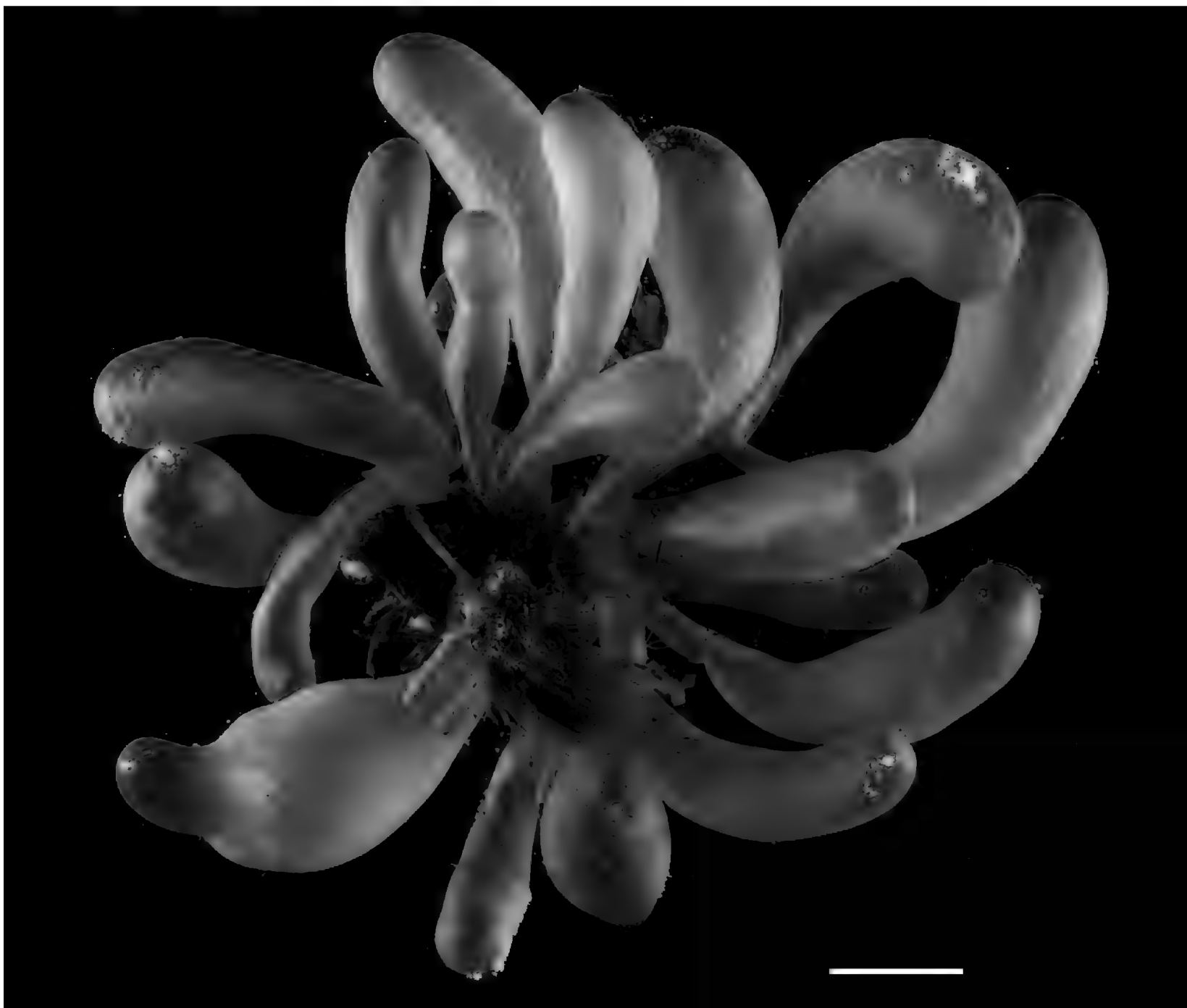


FIGURE 97. *Boergesenia forbesii*. DLB8175: Condado Lagoon, San Juan, 0.2 m. Scale bar = 1.0 cm.

***Boergesenia parvula* D. L. Ballant., H. Ohba, et  
Lozada-Troche**

FIGURE 98

*Boergesenia parvula* D. L. Ballant., H. Ohba, et Lozada-Troche in Ballantine et al. 2011b: 330, figs. 1–6.

*Puerto Rican Record*: Ballantine et al. 2011b.

*Western Atlantic Distribution*: Puerto Rico.

*Type Locality*: Magueyes Island, La Parguera, Puerto Rico.

Plants are vesicular, with vesicles occurring in clusters of 2 or 3 to many. The vesicles are somewhat irregular in shape, being nearly cylindrical to expanded above. They also range from being arcuate to being nearly straight. Individual vesicles measure to 14 mm long and 0.3 to 0.4 mm diam at their bases and to 2.6 mm at their broadest, subapically. The vesicle bases

are variably annularly constricted, the annulations being distinct in some plants and barely discernible in others. Vesicles are rarely branched, occasionally giving rise to another vesicle laterally from near the base. The clusters of vesicles are held together by common entangled rhizoids that measure 60 to 70  $\mu$ m diam. Rhizoids issue from both the base of vesicles as well as from the lower annulate region. The rhizoids terminate in digital pads where they attach to the substratum.

*Habitat and Comments*: *Boergesenia parvula* has been collected only in very shallow water. It was first collected on a marine rail at 10 to 20 cm depth on the west side of Magueyes Island, La Parguera. Subsequently, it was collected at the same depth on rubble, stones, and pieces of wood on silty bottom beneath branches of the mangrove *Rhizophora mangle* L. approximately 100 m north from its original collection site. The species is extremely inconspicuous and known only from the type locality.





FIGURE 98. *Boergesenia parvula*. DLB8170 (isotype): Magueyes Island, La Parguera, <0.5 m. Scale bar = 0.5 cm.

### ***Chamaedoris* Mont.**

*Chamaedoris* Mont. 1842b: 261.

Thalli possess uniseriate elongate stalks that possess annulate thickenings; the stalks are somewhat calcified and bear a brush-like capitulum. The noncalcified capitulum is composed of dichotomously branched filaments that lack basal walls but possess cross walls above each fork.

### ***Chamaedoris peniculum* (J. Ellis et Sol.) Kuntze**

FIGURE 99

*Chamaedoris peniculum* (J. Ellis et Sol.) Kuntze 1898: 400.

*Basionym*: *Corallina peniculum* J. Ellis et Sol. 1786: 127, pl. VII: figs. 5–8, pl. XXV: fig. 1 [these figures of Ellis and Solander were designated as a lectotype by Leliaert et al. 2007: 718].

*Heterotypic Synonym*: *Chamaedoris annulata* Mont. 1842b: 264, nom illeg.

*Puerto Rican Records*: As *Chamaedoris peniculum*: Howe 1915; Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar 1964b; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002; Leliaert and Coppejans 2004.

*Western Atlantic Distribution*: Costa Rica, Mexico, Panama, North America, Bahamas, Barbados, Cuba, Dominica, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, St. Lucia, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: “American seas, particularly near the Bahama Islands.”

Thalli reach 10–20 cm tall, with a cylindrical unbranched stipe, measuring 5.0 cm long or greater and 1.5 mm diam. The stipe possesses conspicuous annular constrictions and plants are attached by rhizoids that originate from the lower portions of the stipes. A terminal noncalcified capitulum is cup shaped to flattened, measuring 3.0–6.5 cm across and 4.0–8.0 mm thick. Capitulum filaments are 80–250 µm diam, arise in whorls, and are highly entangled. Calcium oxalate crystals may be present in the capitulum filaments but are rare. Algae are bright to dark green.

*Habitat and Comments*: Found from shallow water to 25 m depths. In Puerto Rico, most collections have been at a depth of 17 m at the algal plain seaward of Punta Brea, Guánica. [Additional illustrations: as *Chamaedoris annulata*, Harvey 1858: pl. 42B; Vickers 1908: pl. 24; as *Chamaedoris peniculum*, Taylor 1960: pl. 5: fig. 2; Littler and Littler 2000: 331; Leliaert et al. 2007: figs. 32–43; Braune and Guiry 2011: fig. 11.1.]

### ***Dictyosphaeria* Decne.**

*Dictyosphaeria* Decne. 1842b.

Algae are hemispherical, multicellular, solid or hollow; attached by rhizoids from cells near the base. Vegetative cells are usually angular, macroscopic, and coenocytic; increasing in number by segregative division. Cells are attached to each other by minute tentacular cells along the lines of contact. Eleven species of *Dictyosphaeria* are recognized, three of which are known from the Puerto Rican flora.

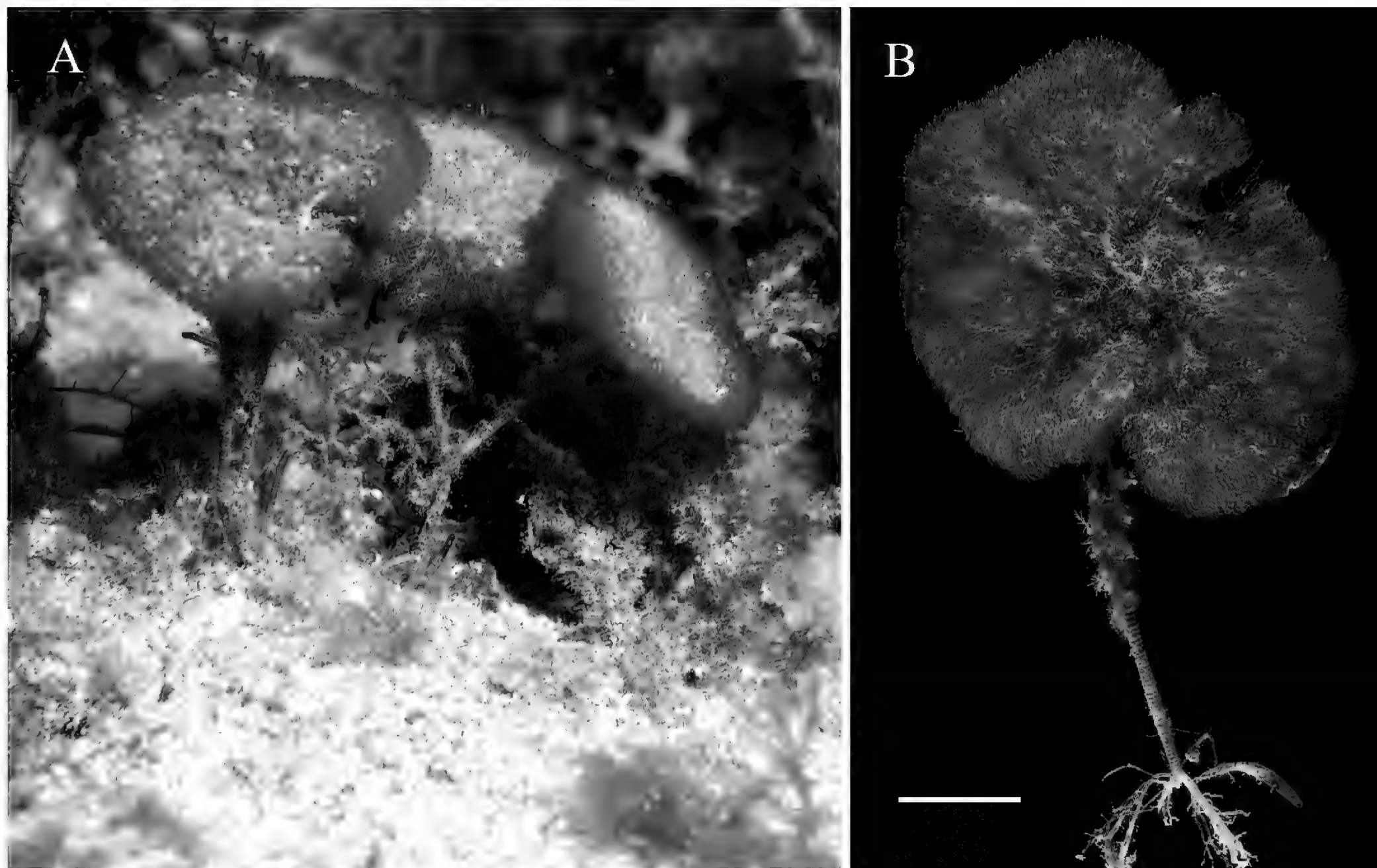


FIGURE 99. *Chamaedoris peniculum*. (A) In situ habit photograph from algal plain offshore from Punta Brea, 15 m. Field = approximately 20 cm. (B). Plant detail. Scale bar = 2.0 cm.

#### KEY TO THE *DICTYOSPHAERIA* SPECIES OF PUERTO RICO

1. Plants large, to 12 cm diameter; thallus hollow, sometimes rupturing and growing as a flat single layer . . . *D. cavernosa*  
Plants smaller . . . . . 2
2. Plants with small lentiform cells at point of contact between vegetative cells; attached by long, prominent rhizoids . . . . .  
. . . . . *D. ocellata*  
Plants not as above; cell wall with spinelike outgrowths . . . . . *D. versluysii*

#### *Dictyosphaeria* sect. *Simplex* Tseng et C. F. Chang

*Dictyosphaeria* sect. *Simplex* Tseng et C. F. Chang 1962: 122, 132.

Species of *D.* sect. *Simplex* are characterized by simple, unbranched hapteroid cells. One member occurs in Puerto Rico.

#### *Dictyosphaeria cavernosa* (Forssk.) Børgesen

FIGURE 100

*Dictyosphaeria cavernosa* (Forssk.) Børgesen 1932: 2, pl. 1: fig. 1.

Basionym: *Ulva cavernosa* Forssk. 1775: 187.

Heterotypic Synonym: *Dictyosphaeria favulosa* (C. Agardh) Decne. ex Endl. 1843: 18.

*Puerto Rican Records:* As *Dictyosphaeria cavernosa*: Taylor 1960; Almodóvar 1962, 1964a; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002. As *Dictyosphaeria favulosa*: Almodóvar and Blomquist 1961.

*Western Atlantic Distribution:* Belize, Costa Rica, Mexico, Panama, North America, Bermuda, Bahamas, Antigua, Barbados, Cayman Islands, Cuba, Dominica, Grenadines, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Nevis, Puerto Rico, St. Barthélemy, St. Eustatius, St. Lucia, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

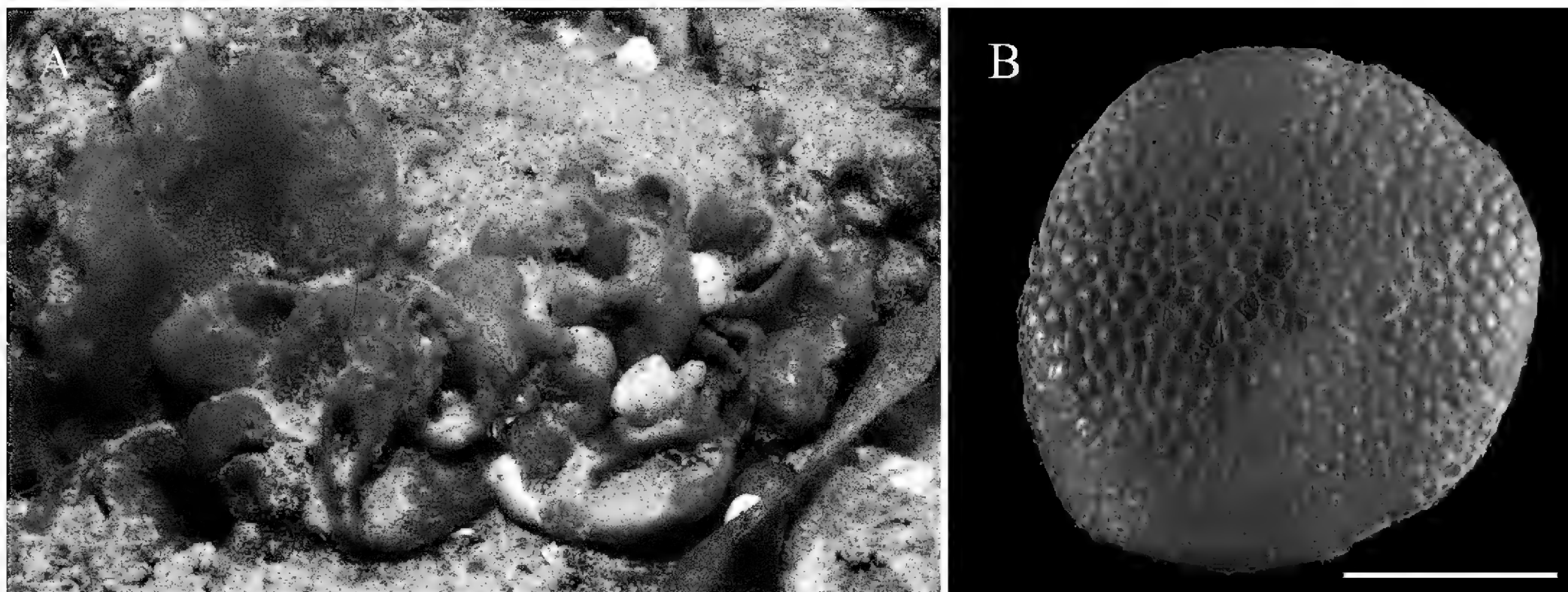


FIGURE 100. *Dictyosphaeria cavernosa*. (A). In situ habit photograph from Turrumote Reef, La Parguera, of an older plant that has split open, 1.0 m. Field = approximately 10 cm. (B) Younger plant, nearly spherical. Scale bar = 1.0 cm.

*Syntype Localities:* Mokha, Yemen [and] “Gomfodae” (Al-Qunfundhah), Saudia Arabia [Mokha, Yemen, fide Leliaert and Coppejans (2004: 202)].

Thalli are multicellular, rounded, rigid, solid or hollow, and saclike to open. Algae are attached by unbranched rhizoids. The thallus is initially small, nearly spherical, 1.0–3.0 cm diam when young, and with maturity, it often becomes open, cuplike or saucer shaped, with irregularly lobed walls that frequently split or may flatten, up 12(–30) cm in extent when mature. The surface wall consists of a single layer of large, macroscopic angular to polygonal cells, 0.1–1.0(–3.0) mm diam, that are attached to each other by minute hapteral cells in rows along lines of contact. Surface cells also contain elongate elliptical to irregularly rod-shaped crystalline structures aggregated in 1 or more cruciate to stellate clusters (Leliaert and Coppejans 2004: table 1, figs. 23–24). Algae are grass green to dark green.

*Habitat and Comments:* *Dictyosphaeria cavernosa* is common in shallow reef areas, often on rocks or dead coral, and occurs from the intertidal and to 55 m depths (Taylor 1960). [Additional illustrations: as *Dictyosphaeria favulosa*, Børgesen 1913: figs. 20a–f, 21a–f, 22; as *Dictyosphaeria favulosa*, Taylor 1960: pl. 7: fig. 5; Braune and Guiry 2011: fig. 12.1.]

### ***Dictyosphaeria* sect. *Ramificata* Tseng et C. F. Chang**

*Dictyosphaeria* sect. *Ramificata* Tseng et C. F. Chang 1962: 126, 132.

Species of *D.* sect. *Ramificata* are characterized by bifurcate to trifurcate branched hapteroid cells. There are two members of this section occurring in Puerto Rico.

### ***Dictyosphaeria ocellata* (M. Howe) J. L. Olsen**

*Dictyosphaeria ocellata* (M. Howe) J. L. Olsen 1985: 62.

*Basionym:* *Valonia ocellata* M. Howe 1920: 603.

*Puerto Rico Records:* As *Dictyosphaeria ocellata*: Ballantine and Aponte 1997a, 2002. As *Valonia ocellata*: Taylor 1960; Almodóvar and Ballantine 1983.

*Western Atlantic Distribution:* Mexico, North America, Bermuda, Bahamas, Barbados, Cayman Islands, Cuba, Guadeloupe, Hispaniola, Martinique, Netherlands Antilles, Puerto Rico, St. Eustatius, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Watling Island, in the Great Sound (=“Great Lagoon”), Warwick Parrish, Bermuda.

Thalli forming cushions or growing in dense clusters, sometimes almost crustose, up to 20 cm in extent and up to 3.0 cm thick, attached by elongated rhizoidal cells conspicuous beneath the surface cells. Globose cells of the upper surface are crowded, irregular to angular, (1–)2.0–4.0 mm diam, and laterally adhered to each other by minute, lentiform hapteral cells, 40–60 µm in diameter.

*Habitat and Comments:* *Dictyosphaeria ocellata* is found on intertidal reef flats and in crevices and epiphytic on mangrove roots in shallow waters. The species is also reported from deeper waters, 30 m depths off the Gulf of Mexico coast of Florida (Dawes and Mathieson 2008). [Illustrations: Taylor 1960: pl. 9: figs. 6, 7; Braune and Guiry 2011: fig. 12.2.]



**Dictyosphaeria versluysii Weber Bosse**

*Dictyosphaeria versluysii* Weber Bosse 1905: 144 (as “*versluysi*”).

*Heterotypic Synonym:* *Dictyosphaeria vanbosseae* Børgesen 1912: 256, figs. 7–9.

*Puerto Rican Records:* As *Dictyosphaeria versluysii*: Ballantine and Aponte 1997a, 2002. As *Dictyosphaeria vanbosseae*: Almodóvar and Ballantine 1983.

*Western Atlantic Distribution:* Mexico, North America, Barbados, Antigua, Cuba, Dominica, Jamaica, Martinique, Puerto Rico, St. Kitts, St. Lucia, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* “Plusiers récifs dans l’Archipel Malaisien.”

Thalli are generally small and nearly spherical, composed of relatively large, angular surface cells in a single layer, mostly ~500(–800) µm diam, laterally adhered to each other by hapteral cells. Surface cells frequently possess internal spinelike projections that are oriented toward the center of the cells, 70–100 µm long. Cell walls are 0.1–1.0(–3.0) mm diam. Algae are grass green in color.

*Habitat and Comments:* *Dictyosphaeria versluysii* occurs in the intertidal and down to 30 m depths. Genetic studies on the Indo-Pacific *D. versluysii* (syntype localities: Malay Archipelago) and Caribbean *D. vanbosseae* Børgesen (type locality: Sandy Point, Cane Bay, St. Croix, U.S. Virgin Islands) will help clarify their phylogenetic relationship. [Illustrations: as *Dictyosphaeria vanbosseae*, Børgesen 1913: figs. 23, 24a,b, 25; as *Dictyosphaeria versluysii*, Tseng and Chang 1962: pl. 1: fig. 9 (variation of intracellular spines); Huisman et al. 2007: 173; Kraft 2007: fig. 48.]

**Ernodesmis Børgesen**

*Ernodesmis* Børgesen 1912: 259.

Thalli are bushy, initiated by a single erect clavate cell, basally somewhat annulate. The stalk cell bears a terminal cluster of similar branch cells, the pattern repeating. The genus is monotypic.

**Ernodesmis verticillata (Kütz.) Børgesen**

FIGURE 101

*Ernodesmis verticillata* (Kütz.) Børgesen 1912: 259, figs. 10–12.

*Basionym:* *Valonia verticillata* Kütz. 1847: 165.

*Puerto Rican Records:* Almodóvar and Blomquist 1961; Almodóvar 1964a; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 2002.

*Western Atlantic Distribution:* Belize, Panama, Mexico, North America, Bermuda, Bahamas, Antigua, Barbados, Cuba, Dominica, Grenadines, Jamaica, Martinique, Monserrate, Netherlands

Antilles, Puerto Rico, St. Eustatius, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* St. Croix, U.S. Virgin Islands.

*Ernodesmis verticillata* is the generitype species. Thalli are bushy, 5.0–10 cm tall, borne on a single initial cell 10–20 mm long and 1.5–2.5 mm diam and attached by small rhizoids. Branching is up to 6 orders, with each branch bearing distally a whorled cluster of up to 12 clavate elongate cells, similar in shape to the initial cells but somewhat smaller.

*Habitat and Comments:* *Ernodesmis verticillata* most commonly occurs in shallow water of sheltered habitats, to a reported depth of 45 m. In Puerto Rico, the species is commonly collected in the seagrass bed windward of Guayacan Island at approximately 1.0 m depth. [Additional illustrations: Kützing 1856: pl. 88; Børgesen 1912: figs. 10–11; Braune and Guiry 2011: fig. 5.1.]

**Siphonocladus F. Schmitz**

*Siphonocladus* F. Schmitz 1879: 18.

Thalli are up to 4.0 cm tall, 1–3 mm diam, composed of many unbranched and branched axes, above a basal portion with prominent basal annular constrictions and well-developed multicellular rhizoids. Thalli are initially a single elongate cell that divides to form a pseudoparenchymatous stalk of appressed polygonal cells that are structurally reinforced by specialized tentacular cells. Uniaxial development in most species is apical and by segregative division. Cell division in rhizoids is by centripetal invagination. The resultant pseudoparenchymatous filament possesses multinucleate cells, 200–500 µm diam, with numerous chloroplasts. Axes are irregularly branched, with many simple and branched lateral branchlets up to 1.0 cm long, in an irregular or whorled branching pattern. One of the seven recognized *Siphonocladus* species is known from Puerto Rico.

**Siphonocladus tropicus (P. Crouan et H. Crouan) J. Agardh**

FIGURE 102

*Siphonocladus tropicus* (P. Crouan et H. Crouan) J. Agardh 1887: 105.

*Basionym:* *Apjohnia tropica* P. Crouan et H. Crouan in Schramm and Mazé 1865: 47; Schramm and Mazé 1866: 113.

*Puerto Rican Records:* As *Siphonocladus tropicus*: Diaz-Piferrer 1963; Almodóvar 1964b; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Panama, North America, Bermuda, Antigua, Barbados, Cuba, Guadeloupe, Jamaica, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).



*Syntype Localities:* “A la plage, mêlé à de vieilles fronds de *Tam-nophora*, sur la coquille du *Strombus gigas*, Marie Galante (Grand-Bourg); [and] Moule de (plage), Basse-Terre” (Schramm and Mazé 1865: 47); Grand-Bourg, SW side of Marie Galante, and Le Moule, NE side of Grande-Terre, Guadeloupe, French West Indies.

*Lectotype:* Leliaert and Coppejans (2004: 203, Appendix 1) listed among the specimens they studied “Mazé 193, Guadeloupe (syntype, BM),” one of two specimens cited in Mazé and Schramm (1878: 105, as *Apjohnia tropica*).

Bushy thalli are erect, solitary or in clusters, and up to 10(–20) cm in height and attached by thick-walled rhizoids. The proximal portion of the stalk is annulate, and the main axes are branched up to 3 orders with numerous branchlets. The main axial (stalk) cell persists, growing up to 5.0 cm in length and becoming 1–3 cells wide and 0.4–1.0 mm diam. Distally, the stalk redivides into many cells and bears numerous long, slender, single-celled branchlets, 1.0–2.0 cm long and 300–500 µm diam. Algae are pale green in color.

*Habitat and Comments:* *Siphonocladus tropicus* is generally found in shallow waters of protected habitats, epiphytic on other algae, and growing on calcareous substrata or unattached and drifting on the bottom. In southwestern Puerto Rico, *S. tropicus* occurs on the algal plain at Punta Brea at 17 m depth. [Additional illustrations: Vickers 1908: pl. 18; Joly et al. 1976: figs. 16–20; Bula-Meyer 1982: pl. 2: figs. 5–6, pl. 9: fig. 39.]

## VALONIACEAE KÜTZ.

### *Valonia* C. Agardh

*Valonia* C. Agardh 1823: 428.

Thalli of coenocytic, multinucleate vesicles that are solitary vesicles or few to many, attached below by smaller hapteral or rhizoidal cells. The thallus is sometimes limited to the original vegetative cell, or in other species its divisions and redivisions into similar cells form clusters or masses of vesicles. Nine species of *Valonia* are recognized worldwide, of which four are known to Puerto Rico.

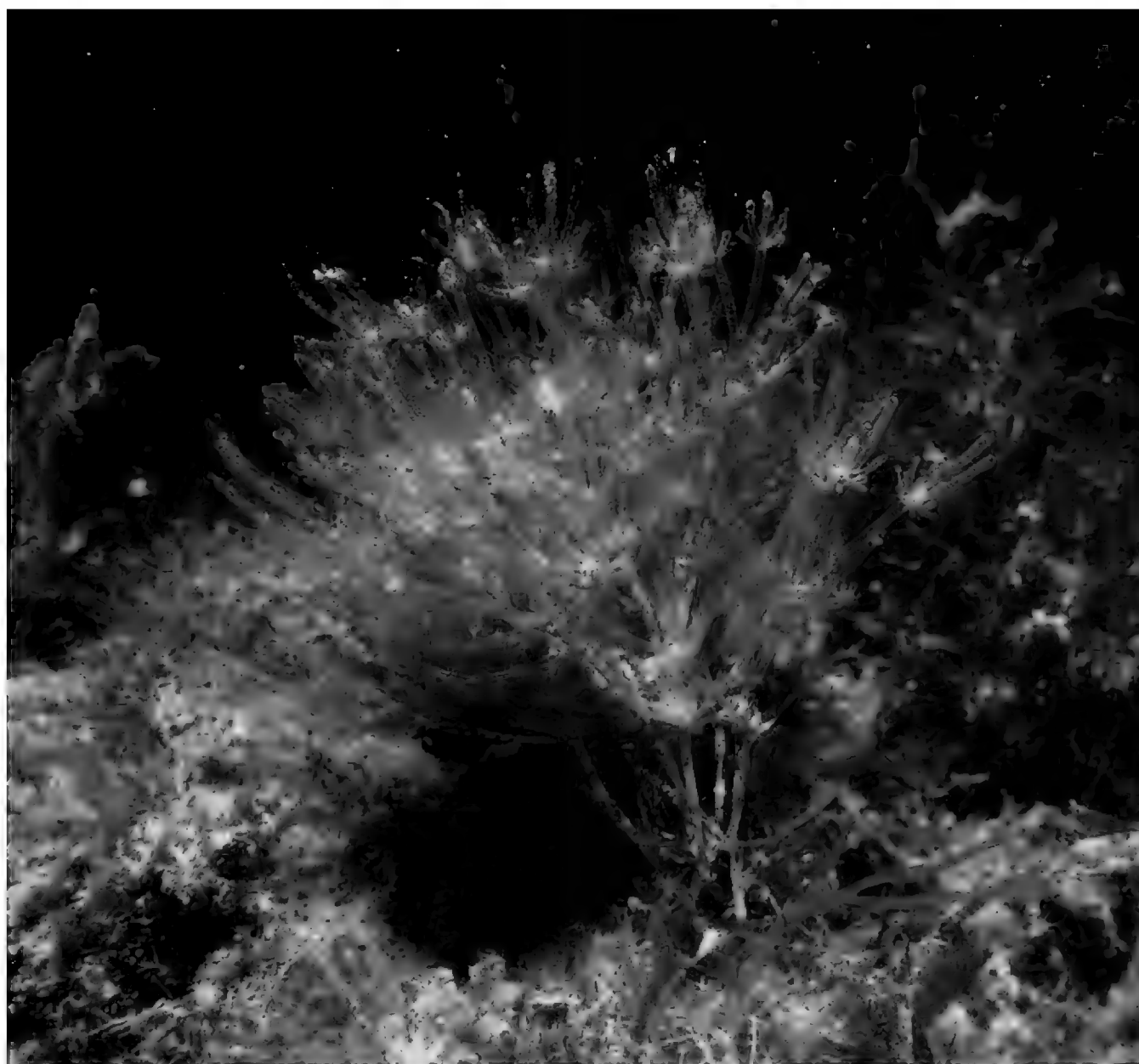


FIGURE 101. *Ernodesmis verticillata*. In situ habit photograph from algal plain offshore from Punta Brea, 15 m. Field = approximately 10.0 cm.

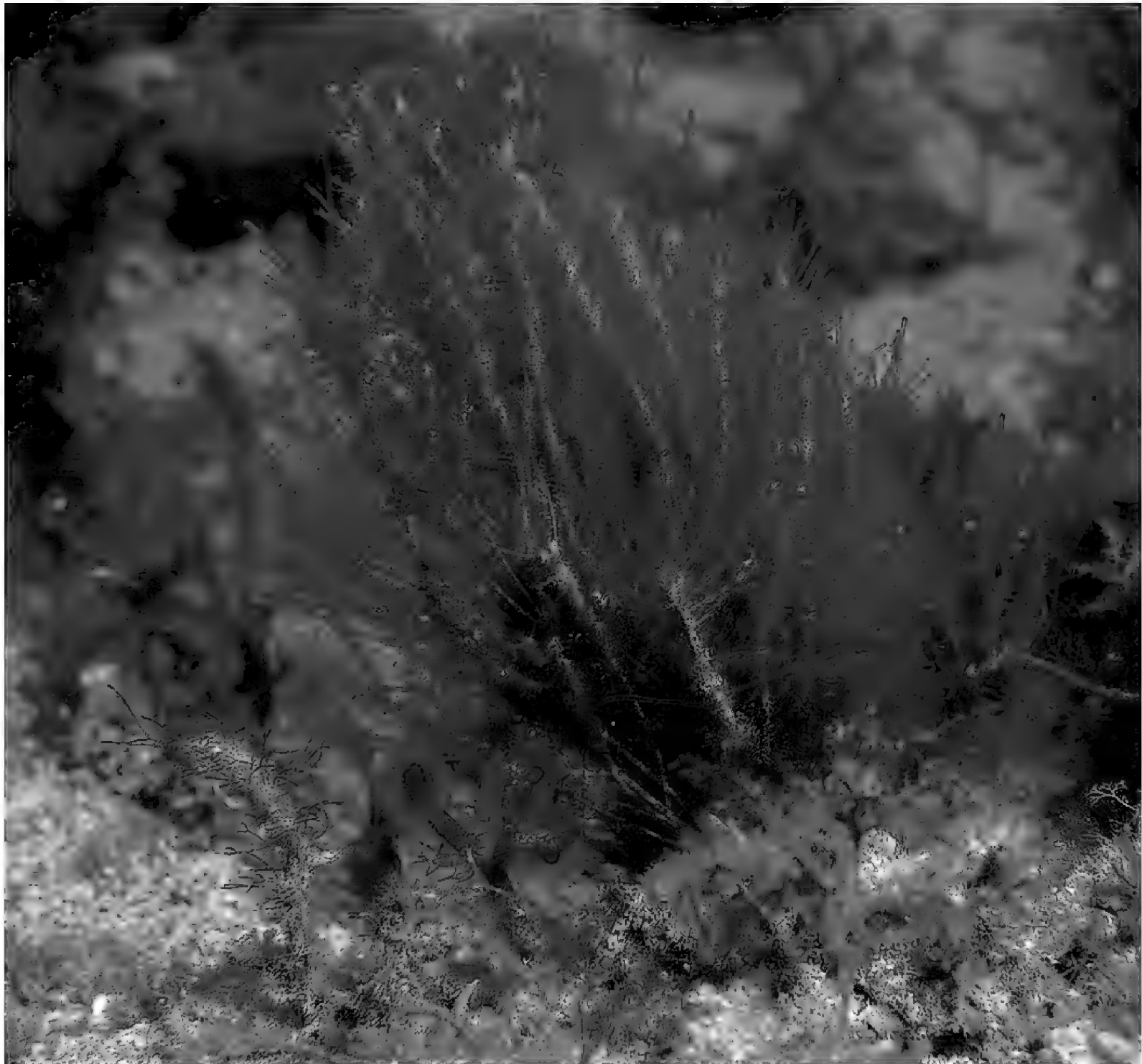


FIGURE 102. *Siphonocladus tropicus*. In situ habit photograph from algal plain offshore from Punta Brea, 15 m. Field = approximately 20 cm.

KEY TO THE VALONIA SPECIES OF PUERTO RICO

- 1. Plants large, to 12 cm diam; thallus hollow, sometimes rupturing and growing as a flat single layer . . . . . *V. ventricosa*  
Thalli of few to many vegetative cells, individual cell size generally less than 15 mm diam . . . . . 2
- 2. Thallus distinctly filamentous; cells less than 5 mm in diameter . . . . . 3  
Thalli of clusters of ovoid cells (1.0–)2.0–4.0 cm in extent; individual cells 5–15 mm in diameter . . . . . *V. macrophysa*
- 3. Filaments principally erect with mostly subcylindrical cells . . . . . *V. aegagropila*  
Filaments at least initially creeping, cells may be clavate and frequently arcuate . . . . . *V. utricularis*

**Valonia aegagropila C. Agardh**

*Valonia aegagropila* C. Agardh 1823: 429.

*Puerto Rican Records:* Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar 1962, 1964a; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Belize, North America, Bahamas, Cuba, Hispaniola, Honduras, Jamaica, Netherlands Antilles, Nevis, Puerto Rico, St. Barthélemy, Turks and Caicos, U.S. Virgin Islands, Brazil, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Syntype Localities:* “In lacuna Veneta copiose natans. In mari Australi ad JRavak” (Agardh 1823: 429).

*Lectotype Locality:* Lagoon; Venice, Adriatic Sea, northern Italy, Mediterranean Sea, fide Egerod (1952; see also Olsen and West 1988; Silva et al. 1996; Leliaert and Coppejans 2004).

*Valonia aegagropila* is the generitype species. Thalli are composed of small, closely packed, angular cells (honeycomb-like in surface view) that form cushion-like clumps to expanding masses, 4.0–20 mm in diameter, attached to the substratum by minute rhizoids. Individual cells are 1.0–3.0 mm diam and 5.0–10(–20) mm long, with an expanded upper region and a lower subcylindrical portion that is straight or arcuate and branched. Algae are bright to dark green in color.

*Habitat and Comments:* *Valonia aegagropila* occurs in shallow-water habitats and protected lagoons, down to 7 m depths. It forms large, unattached balls in lagoons in Italy (Cormaci et al. 2014). [Illustrations: Taylor 1960: pl. 7: fig. 6; Huisman et al. 2007: fig. 31; Cormaci et al. 2014: pl. 86: figs. 4–5.]

### ***Valonia macrophysa* Kütz.**

FIGURE 103

*Valonia macrophysa* Kütz. 1843: 307.

*Puerto Rican Records:* Diaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution:* Belize, Mexico, Panama, North America, Bermuda, Bahamas, Antigua, Barbados, Cayman Islands, Cuba, Grenadines, Jamaica, Martinique, Netherlands Antilles, Nevis, Puerto Rico, St. Eustatius, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Venezuela.

*World Records:* See Guiry and Guiry (2022).

*Type Locality:* “Insel Lessina, im Adriatischen Meere” [Hvar Island (=Lesina), off Dalmatian coast, Croatia, Adriatic Sea].

Thalli consist of crowded clusters of adhered cells that may become 2.0–5.0 cm thick and frequently cover a significant area, attached by rhizoids. Cells are creeping, crowded together and adherent. They are ovoid to obovate or irregular in shape and branch from near the base or exposed sides. The vegetative cells measure 0.5–1.5 cm diam and generally are (1.0–)2.0(–4.0) cm long. Algae are dark green to olive green in color.

*Habitat and Comments:* *Valonia macrophysa* occurs on rocks, reefs, and mangroves in shallow water from the lower intertidal to the deep subtidal. In Puerto Rico, *V. macrophysa* is common as heavy growth on prop roots of *Rhizophora* in the mangrove channels at Guayacan Island. Generally considered a shallow-water species, it has also been reported from 82 m in Puerto Rico (Ballantine et al. 2016) and in the Bahamas to 76 m at Lee Stocking Island (Ballantine and Aponte 2003) and to 92 m depths off San Salvador Island (Norris and Olsen 1991). [Additional illustrations: Cormaci et al. 2014: fig. 1A,B.]



FIGURE 103. *Valonia macrophysa*. In situ on *Rhizophora* mangle prop roots, leeward Guayacan Island, La Parguera. Field = approximately 25 cm.

### ***Valonia utricularis* (Roth) C. Agardh**

*Valonia utricularis* (Roth) C. Agardh 1823: 431.

*Basionym:* *Conferva utricularis* Roth 1797: 160, pl. 1: fig. 1.

*Puerto Rican Records:* As *Valonia utricularis*: Diaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Panama, North America, Bermuda, Bahamas, Cuba, Guadeloupe, Hispaniola, Honduras, Jamaica, Martinique, Puerto Rico, St. Barthélemy, St. Eustatius, Trinidad and Tobago, U.S. Virgin Islands, Brazil.

*World Distribution:* See Guiry and Guiry (2022).

*Syntype Localities:* “In maris mediterranei.”

Thalli are composed of short to long, randomly arranged branched axes of large cylindrical, clavate, or sometimes arcuate cells, 5.0–20 mm long and 1.0–2.5 mm in diameter, that produce branches from the apical end. Developing from a creeping habit, they later become erect and up to 5.0 cm tall at maturity. Algae are bright green.



*Habitat and Comments:* *Valonia utricularis* is found in shallow water on reefs in protected habitats, to 5.0 m depth. [Illustrations: Børgesen 1913: fig. 17; Braune and Guiry 2011: fig. 16.2; Cormaci et al. 2014: 386FP, figs. 3–4.]

### ***Valonia ventricosa* J. Agardh**

FIGURE 104

*Valonia ventricosa* J. Agardh 1887: 96.

*Homotypic Synonym:* *Ventricaria ventricosa* (J. Agardh) J. L. Olsen et J. A. West 1988: 104, figs. 1–4, 11.

*Puerto Rican Records:* As *Valonia ventricosa*: Almodóvar and Blomquist 1959; Taylor 1960; Almodóvar 1962; Schwartz and Almodóvar 1971; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Hinds and Ballantine 1987; Ballantine et al. 2016. As *Ventricaria ventricosa*: Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Belize, Costa Rica, Mexico, Panama, North America, Bermuda, Bahamas, Barbados, Cayman Islands, Cuba, Grenadines, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Nevis, Puerto Rico, St. Eustatius, St. Kitts, St. Lucia, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Syntype Localities:* “In mari Indiae occidentalis ad Insulani Stae Crucis ad Guadeloupe” (Agardh 1887: 96).

*Lectotype Locality:* Guadeloupe, West Indies (Olsen and West 1988).

Thalli are solitary or of a few cells together, most commonly constituting a single large oval, spherical, or pyriform cell measuring 1.5–3.0(–10) cm diam. The principal vegetative cell is attached to the substratum by small proximal hapteral cells. Algae are glossy and dark green in color.

*Habitat and Comments:* *Valonia ventricosa* is common in shallow-water habitats and in deep water at 36–100 m depths in Puerto Rico (Ballantine et al. 2016). In La Parguera, *V. ventricosa*



FIGURE 104. *Valonia ventricosa*. In situ habit photograph from edge of insular shelf, offshore from La Parguera, cluster of coenocytic cells. Field = approximately 30 cm.



is common among mangroves, either attached or drifting among *Rhizophora* prop roots. In the Florida Keys it was one of the dominant species in deep water from 30 to 70 m depths (Leichter et al. 2008). [Additional illustrations: Braune and Guiry 2011: fig. 14.1; Cormaci et al. 2014: pl. 88: figs. 2–3.]

### **DASYCLADALES PASHER**

### **DASYCLADACEAE KÜTZ.**

### ***Batophora* J. Agardh**

*Batophora* J. Agardh 1854: 107.

Thalli are noncalcified unicells up to 10 cm tall, composed of an erect, nonbranched axial cell, bearing whorls of short, determinate branchlets. The determinate branchlets are repeatedly di- to trichotomously branched up to 7 orders. Uppermost hair-like branchlets are branched up to 4 orders. Algae are attached by rhizoidal outgrowths at the base of axial cells. Gametangia are spherical, developing from the branching nodes of the lateral branchlets. Gametangia are homologous to rays of *Acetabularia* and form uninucleate cysts. There are two recognized *Batophora* species, one of which is known from Puerto Rico.

### ***Batophora oerstedii* J. Agardh**

FIGURE 105

*Batophora oerstedii* J. Agardh 1854: 108.

*Puerto Rican Records:* Almodóvar and Blomquist 1961; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Belize, North America, Bermuda, Bahamas, Barbuda, Cuba, Guadeloupe, Hispaniola, Honduras, Jamaica, Netherlands Antilles, Puerto Rico, St. Martin, Turks and Caicos, U.S. Virgin Islands, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* “Hab. ad radices *Rhizophorae* Mangle in sinu substagnanti, ‘Krauses lagoon’ dicto, ad Insulam St. Crucis” (J. Agardh 1854: 108); on prop roots of *Rhizophora*; Krause Lagoon, St. Croix, U.S. Virgin Islands.

*Batophora oerstedii* is the generitype species. Thalli are soft and delicate, growing in clusters or spreading over the substratum. Individual thalli possess an erect, simple axis, 4.0–6.0(–14) cm high, bearing 8–10 whorls of monosiphonous branchlets, 4.0–10 mm diam. Branchlets are absent in lower portions, and plants are attached basally by lobed rhizoidal outgrowths. Lateral branchlets are short, 0.5–2.0 mm apart, and dichotomously branched to 6 or 7 orders, with terminal hairlike laterals that are branched to 2–3 orders. Gametophores are yellow green and oval to elliptical, measuring 30–700 µm diam and 500–1,000



FIGURE 105. *Batophora oerstedii*. LRAsn, herbarium specimen: Saline lagoon, Guayacan Island. Scale bar = 2.0 cm.

µm long. They are borne on the inner dichotomies of the first-order whorled branchlets and develop numerous gametangia, 40–50(–75) µm diam. Algae are bright green in color.

*Habitat and Comments:* Found in quiet lagoons, the species is typically on the borders of mangrove thickets in shallow water near the low-tide level. Algae may form extensive carpets on mangrove peat in very shallow environments. In the La Parguera region, the species is commonly collected in the lee of Guayacan Island. [Additional illustrations: Berger and Kaeffer 1992: fig. 3.16a; Berger 2006: figs. 12–28; Littler et al. 2008: 232; Braune and Guiry 2011: fig. 26.1.]

### ***Cymopolia* J. V. Lamour.**

*Cymopolia* J. V. Lamour. 1816: 292.

Thalli are erect, siphonous, multinucleate axes that are either unbranched or dichotomously branched. The axes are composed of a series of calcified segments, up to 4.0 mm diam, separated by flexible uncalcified joints. Attachment is by dense clusters of rhizoids produced from the lower segments. Axes are

constricted at regular intervals, with calcified segments bearing whorls of corticating determinate branchlets. Axes and branches terminate in delicate, bright-green whorls of deciduous tufts of sterile hairs, branched up to 3 times. The smooth calcified surface of the segments is developed from clusters of 4–8 distal club-shaped cells that are laterally adherent. Cells possess numerous discoid, parietal chloroplasts without pyrenoids, and starch grains in both chloroplasts and cytoplasm are not membrane bound. Two *Cymopolia* species are recognized, one of which is known from Puerto Rico.

***Cymopolia barbata* (L.) J. V. Lamour.**

FIGURE 106

*Cymopolia barbata* (L.) J. V. Lamour. 1816: 293.

*Basionym:* *Corallina barbata* L. 1758: 806 [a lectotype illustration from Ellis (1755: 53–54, pl. 25C) was selected by L. Irvine in Spencer et al. (2009: 245)].

*Puerto Rican Records:* As *Cymopolia barbata*: Howe 1915; Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* North America, Bermuda, Bahamas, Antigua, Cuba, Hispaniola, Jamaica, Puerto Rico, Turks and Caicos, Colombia, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* “Hab. Oc. Americano.”

*Cymopolia barbata* is the generitype species. Thalli are 10–30 cm tall with terete segmented axes. Segments measure 2.0–4.0 mm diam and 3.0–11 mm long; they are moderately calcified and white with lime. Cells in surface view appear club shaped, 115–125  $\mu\text{m}$  diam. Axes are terminated by conspicuous tufts of noncalcified filaments that fork 5–6 times with the distal divisions being hairlike, each hair cell divided up to 5–6 times. Sporangia are solitary, lying between cells of the outer cortical zone; they are spherical to pyriform in shape, 150–200  $\mu\text{m}$  diam. Algae are grass green to white in color.

*Habitat and Comments:* *Cymopolia barbata* is a shallow-water species. On the south coast of Puerto Rico, the species has been collected only at Caja de Muertos. It is more commonly seen in north coast habitats, being common in shallow water at Crashboat, Aguadilla. [Additional illustrations: Harvey 1858: pl. 41A; Berger and Kaever 1992: fig. 3.41a,b.]

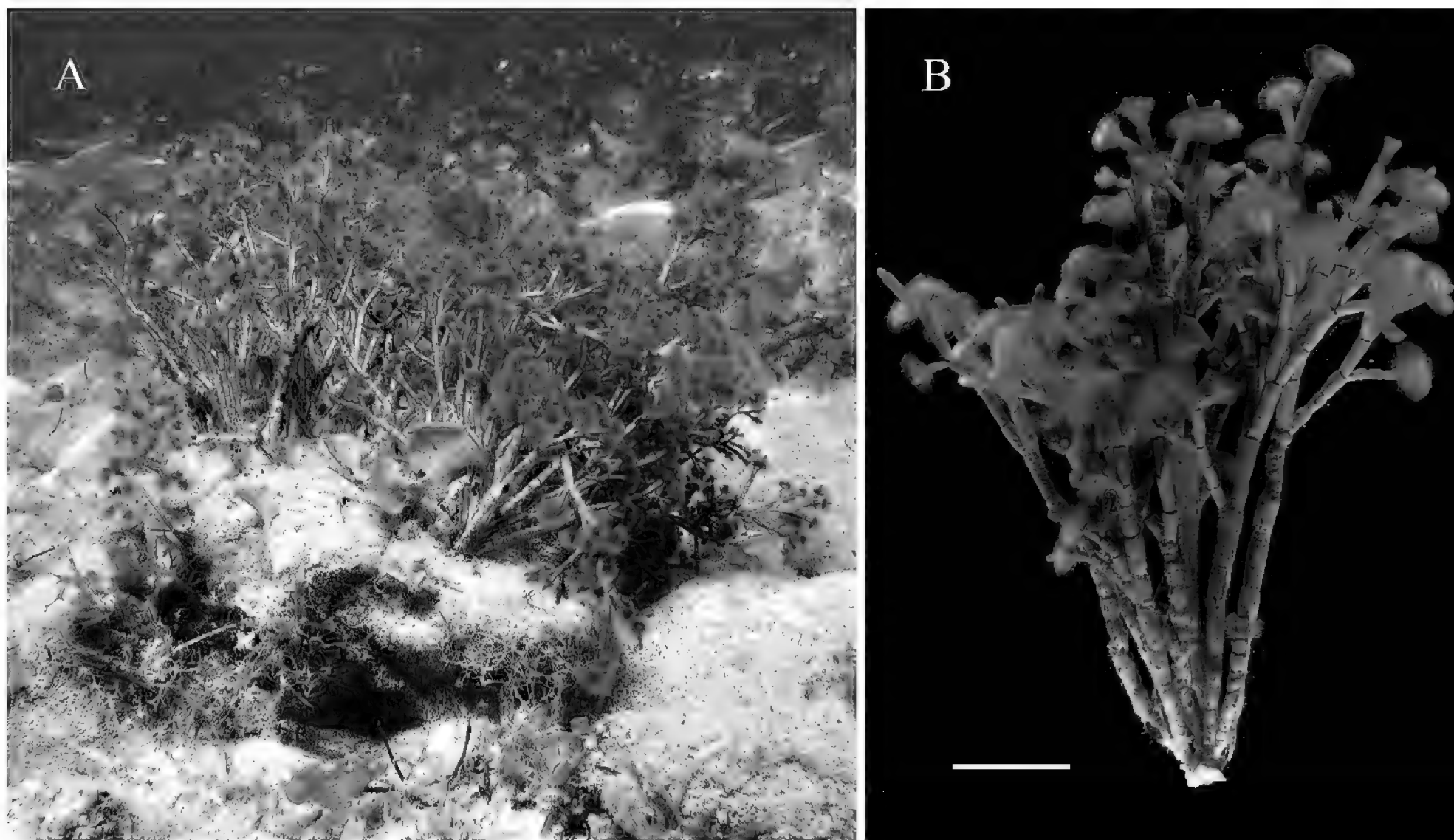


FIGURE 106. *Cymopolia barbata*. (A) In situ photograph at Crashboat, Aguadilla. Field = approximately 20 cm. (B) Detail of plant. Scale bar = 2.0 cm.

## ***Dasycladus* C. Agardh**

*Dasycladus* C. Agardh 1828: 15.

Thalli are unicellular, up to 6 cm tall, composed of unbranched, noncalcified, elongate axes that bears dense, compact whorls of short, determinate lateral branchlets. The branchlets are dichotomously to trichotomously branched, to 3 orders. Axes become calcified at their base, and numerous rhizoidal branches attach the plant to the substratum. Thalli possess a spongy consistency. Gametangia are solitary, terminal on basal cells of the whorl branchlets. Algae are olive green in color. One *Dasycladus* species is known from Puerto Rico, and three species are recognized worldwide.

### ***Dasycladus vermicularis* (Scop.) Krasser**

*Dasycladus vermicularis* (Scop.) Krasser in Beck and Zahlbruckner 1898: 459.

*Basionym*: *Spongia vermicularis* Scop. 1772: 412, pl. 64: fig. 1454.

*Puerto Rican Records*: As *Dasycladus vermicularis*: Diaz-Piferer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution*: Belize, North America, Bermuda, Bahamas, Cayman Islands, Cuba, Hispaniola, Jamaica, Martinique, Puerto Rico, Trinidad and Tobago, Turks and Caicos, Brazil.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: “Habitat ibidem super lapides et conches.”

Thalli are 2.0–6.0 cm tall, with an axial cell, bearing compact whorls of 10–15 short, closely set, lateral branchlets, in clusters about 3.0–6.0 mm diam. The lower axes are naked and attached by rhizoidal lobes. The basal cell of each lateral

branchlet is di- to trichotomously divided 3–4 times and terminates with a filiform or short spikelike apical cell surrounded by compact whorls of branchlet clusters. Algae are green in color.

*Habitat and Comments*: *Dasycladus vermicularis* occurs mostly in shallow water in exposed habitats, such as the low intertidal on reefs and in tide pools. The species has also been dredged from 50 m depths in the Florida Keys (Taylor 1960; Dawes and Mathieson 2008) and the Bermudan Challenger Bank (Frederick 1963). [Illustrations: Berger and Kaeffer 1992: fig. 3.6a,b; Berger 2006: figs. 75–82; Braune and Guiry 2011: fig. 29.1.]

## ***Neomeris* J. V. Lamour.**

*Neomeris* J. V. Lamour. 1816: 243.

Thalli occur solitarily or grow in groups. Each thallus consists of a small cylindrical or club-shaped, unbranched unicell, calcified in ringlike segmented bands, up to 3.0 cm tall. Axes are attached to the substratum by rhizoidal outgrowths. The erect axes upwardly bear closely placed whorls of short laterals that branch to 3 orders and an apical tuft of noncalcified hairs. Cells possess numerous discoid, parietal chloroplasts without pyrenoids. Non-membrane-bound starch grains occur both inside and outside of plastids. First-order laterals are either free or coherent, depending on the species. Secondary laterals are modified to form 2 cells with faceted surfaces barely protruding above the surface calcification and a single uninucleate gametangium. Each gametangium develops a single cyst that divides multiple times to produce biflagellate gametes that are later released through an operculum. Two *Neomeris* species are known from Puerto Rico, and nine species are recognized worldwide.

### **KEY TO THE *NEOMERIS* SPECIES OF PUERTO RICO**

1. Gametangia are laterally coherent . . . . . *N. annulata*  
Gametangia are mutually free . . . . . *N. mucosa*

### ***Neomeris annulata* Dickie**

FIGURE 107

*Neomeris annulata* Dickie 1874c: 198.

*Puerto Rican Records*: Almodóvar and Blomquist 1959, 1961; Taylor 1960; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution*: Belize, Costa Rica, Panama, North America, Bermuda, Bahamas, Barbados, Antigua,

Barbados, Cuba, Dominica, Netherlands Antilles, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Nevis, Puerto Rico, St. Eustatius, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Mauritius.

Thalli are occasionally solitary, occurring more commonly in clusters. Individuals measure 1.0–3.0 cm tall and 1.0–2.0 mm diam. Mature algae are substantially calcified below, less heavily above. Axial cells, 400–640 µm diam, bear closely packed branchlet whorls that each bear 2 capitate polyhedral branchlet cells, 80–135 µm diam in surface view, forming the fairly even





FIGURE 107. *Neomeris annulata*. In situ habit photograph from algal plain offshore from Media Luna Reef, 17 m. Field = approximately 20 cm.

faceted surface. Apices bear tufts of deciduous simple hairs. Sporangia are obovate, with a simple oval aplanospore, 46–80  $\mu\text{m}$  diam and 115–175  $\mu\text{m}$  long, and are cut off between the polyhedral branchlet cells. The algae are proximally white because of heavy calcification, becoming light green toward and at the apex.

**Habitat and Comments:** Although *Neomeris annulata* is typically reported from shallow-water habitats (on coral or shell fragments in shallow, sandy habitats), Taylor (1960) and Dawes and Mathieson (2008) indicated a maximum depth of 50 m for the species; in Puerto Rico, it has been collected to a depth of 46 m (Ballantine et al. 2016). [Additional illustrations: Taylor 1960: pl. 5: fig. 5, pl. 6: figs. 4–6; Norris and Bucher 1982: fig. 91; Berger and Kaever 1992: fig. 3.35a; Cormaci et al. 2014: 288FP, figs. 4–5.]

### ***Neomeris mucosa* M. Howe**

*Neomeris mucosa* M. Howe 1909: 84, pl. 1: fig. 5, pl. 5: figs. 1–14.

*Puerto Rican Record:* Almodóvar 1970.

**Western Atlantic Distribution:** Belize, Bahamas, Antigua, Cuba, Netherlands Antilles, Puerto Rico, Turks and Caicos.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Samana Cay (=Atwood Cay), Bahamas.

Thalli possess a subcylindrical or fusiform axis, measuring 8.0–20 mm tall and 1.5–2.5 mm diam. The primary axes cut off numerous whorls of short branchlets, and apical tufts consist of inconspicuous ditrichotomous deciduous hairs. Branchlets of the primary whorls each bear 2 capitate polyhedral branchlet cells, 100–200  $\mu\text{m}$  diam in surface view, that form the facets of the continuous cortex. Gametangia are strongly calcified but mutually free. They measure 178–215  $\mu\text{m}$  long including the stalk, and the aplanospores measure 104–121  $\mu\text{m}$  diam and 140–160  $\mu\text{m}$  long. Algae are green above, grayish white below in color.

**Habitat and Comments:** *Neomeris mucosa* is found in moderately exposed habitats, near the low-water mark. [Illustration: Littler and Littler 2000: 441.]



**POLYPHYSACEAE KÜTZ.**

Polyphysaceae Kütz. 1843: 302.

***Acetabularia* J. V. Lamour.**

*Acetabularia* J. V. Lamour. 1812, nom. cons.

Thalli are calcified and grow erect from a rhizoidal base. The slender axial cells are cylindrical or have slight annulate

thickenings and are uninucleate. They bear at the summit, up to 3 terminal caps, composed of whorl branchlet cells constituting cap rays. These are laterally fused or not. Caps rays are produced from primordia near the stalk that become lobed and develop a corona superior (dorsal/upper side at base of ray) and a corona inferior (ventral/lower side at base of ray). Fertile rays produce gametangial cysts that are noncalcified, calcified, or surrounded by calcified spicules and contain gametes at maturity. There are 3 *Acetabularia* species known from Puerto Rico, and 13 species are known worldwide.

**KEY TO ACETABULARIA SPECIES OF PUERTO RICO**

1. Disc with 22–30 rays, to 7.0 mm diam ..... *A. caliculus*  
     Disc with 30 or more rays, 5.0–20 mm diam ..... 2
2. Plants to 7 cm tall; discs 12–20 mm diam ..... *A. crenulata*  
     Plants to 3 cm tall; discs 3.0–8.0 mm diam ..... *A. schenckii*

***Acetabularia* subgen. *Acicularia* (d'Archiac) S. Berger, Fettweiss, S. Gleissberg, Liddle, U. Richt., Sawitzky, et Zuccarello**

*Acetabularia* subgen. *Acicularia* (d'Archiac) S. Berger, Fettweiss, S. Gleissberg, Liddle, U. Richt., Sawitzky, et Zuccarello 2003: 560.

*Basionym*: *Acicularia* d'Archiac 1843: 386, 388, pl. XXV: fig. 8a.

*Notes*: Taxonomically, *Acetabularia* subgen. *Acicularia* includes all species of *Acetabularia* that have unfused cap primordia (Berger et al. 2003: 560). It differs morphologically from *Acetabularia* subgen. *Acetabularia*, which has congenitally fused cap primordia (Berger et al. 2003: 559) and is currently a monotypic subgenus based on the generitype *A. acetabulum* (Linnaeus) P. C. Silva 1952: 255.

*Acicularia* is a genus of only fossil species (e.g., Egerod 1952; Bailey et al. 1976; Berger et al. 2003; Guiry and Guiry 2022). Some confusion was created by Berger et al. (2003) in using the generic name twice in the same publication for different taxa, first in using *Acicularia* d'Archiac (1843) as an accepted genus (Berger et al. 2003: 529) and then later as the basionym for their proposed *Acetabularia* subgen. *Acicularia* (d'Archiac) S. Berger et al. (2003: 560).

All three Puerto Rican *Acetabularia* species are members of *Acetabularia* subgen. *Acicularia*.

***Acetabularia caliculus* J. V. Lamour.**

FIGURE 108

*Acetabularia caliculus* J. V. Lamour. in Quoy et Gaimard 1824: 621. [Note that although the species name has sometimes been spelled “*calyculus*,” the correct spelling is *caliculus* (Berger et al. 2003; Norris 2010).]

*Puerto Rican Records*: As *Acetabularia calyculus*: Diaz-Piferer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution*: Costa Rica, North America, Cuba, Jamaica, Netherlands Antilles, Puerto Rico, St. Eustatius, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Shark Bay, Western Australia.

Solitary or in clusters, thalli are 1.5–3.0 cm tall. The lightly calcified axial cell is 200–250 µm diam proximally and 350–400 µm diam distally. The stalks bear whorls of (5–)10–16 deciduous, hairlike branched filaments leaving only scars at maturity and a distinct cup-shaped terminal cap. The apical caps are cup shaped, 4.0–7.0 mm diam, composed of (20–)22–35 rays, laterally joined by calcification, each ray 2.0–3.0 mm long and 70–160 µm diam near the base and 400–520 µm in diameter near the apex. The distal ends of each ray are emarginate or ultimately with a broad square notch. The corona superior is composed of short projections with blunt lobes and 2–3(–4) colorless hairs or hair scars. Fertile rays produce bright-green, spherical to subspherical, noncalcified, gametangial cysts, each (80–)120–160 µm diam, numbering (25–)45–80 per ray. The corona inferior consists of short, inconspicuous, oblong blunt lobes. Algae are bright green in color with a whitish stalk.

*Habitat and Comments*: *Acetabularia caliculus* mostly occurs in shallow water to 5.0 m depth in sheltered habitats on mangrove prop roots and attached to shells, coral fragments, or small rocks in the sand-silt sediment of seagrass beds and mudflats and on exposed reefs. [Additional illustrations: Børgesen 1908: figs. 4–7; Berger and Kaever 1992: fig. 3.67a–e; Littler et al. 2008: 233; Norris 2010: fig. 49; Cormaci et al. 2014: 292FP, figs. 4–8.]



FIGURE 108. *Acetabularia caliculus*. MDP20336, herbarium specimen: Gulf of Cariaco, Sucre State, Venezuela. Scale bar = 1.0 cm.

***Acetabularia crenulata*** J. V. Lamour.

FIGURE 109

*Acetabularia crenulata* J. V. Lamour. 1816: 249, pl. 8: fig. 1.

**Puerto Rican Records:** Taylor 1960; Almodóvar 1964a, 1971; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002.

**Western Atlantic Distribution:** Belize, Costa Rica, Panama, Mexico, North America, Bermuda, Bahamas, Barbados, Cayman Islands, Cuba, Guadeloupe, Hispaniola, Honduras, Jamaica, Netherlands Antilles, Puerto Rico, St. Eustatius, St. Martin, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Caribbean Sea (Silva et al. 1996).

Thalli are solitary or clustered, reaching 2.0–8.0 cm tall. Stalks are heavily calcified, 2.0–7.0 mm long and 200–300(–600)

µm diam, and attached to substratum by basal lobed outgrowths. Terminal caps are at first funnel shaped, becoming nearly flat, measuring 4.0–20 mm diam, and composed of 20–80 coherent rays. Cap rays measure 2.0–6.5 mm long and 50–120 µm diam at the base and 200–650 µm diam near the apex. The distal walls of cap rays are truncate, commonly with a median apiculus. The upper portion of stalks may also have whorls of deciduous hairlike filaments. The corona superior possesses elongate, deeply indented lobes, each with 2–3 hair scars. The corona inferior has digitate-like projections on the lower side of ray bases. At maturity, up to 500 cysts are produced per cap ray, each 60–80(–100) µm diam.

**Habitat and Comments:** *Acetabularia crenulata* occurs on rocks, rubble, and coral fragments in shallow, protected lagoons, often on the borders of mangrove as well as on mangrove roots, on reef platforms in tide pools, and among seagrasses. In Puerto Rico, the species may be found on *Rhizophora* prop roots at the lee of Guayacan Island as well as at a hypersaline lagoon within Guayacan Island. [Additional illustrations: Harvey 1858: pl. 42A; Bailey et al. 1976: figs. 14–17; Berger and Kaever 1992:

fig. 3.16a–f; Berger 2006: figs. 125–145, 313, 323; Littler et al. 2008: 235; Moura et al. 2014: fig. 3A–H.]

### ***Acetabularia schenckii* Möbius**

*Acetabularia schenckii* Möbius 1889: 320.

*Homotypic Synonym:* *Acicularia schenckii* (Möbius) Solms-Laubach 1895: 33, pl. 3: figs. 4, 9, 11–12, 14–15.

*Puerto Rican Records:* Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Panama, North America, Bermuda, Bahamas, Barbados, Cuba, Guadeloupe, Hispaniola, Martinique, Puerto Rico, St. Eustatius, U.S. Virgin Islands, Brazil, Colombia.

*Type Locality:* Cabo Frio, Brazil.

Thalli are 3.0–8.0 cm tall and usually growing in clusters or rarely solitary. The stalks, 6.0–28 mm long and 420–600 µm diam, are heavily calcified and are attached basally to substratum by lobed outgrowths. Stalks terminally bear 1 or more cup-shaped or flattened caps, 5.0–20 mm diam composed of

30–60 closely united, wedge-shaped rays. The rays are apiculate distally, where they are 60–80 µm diam. Stalks may also have whorls of deciduous hairlike filaments. The corona superior with a deep cleft on each segment is composed of cuneiform to oblong segments, 120–190 µm diam, bearing 2–3 hairs or hair scars. The corona inferior is of oblong, rounded, or bilobed segments, 110–150 µm diam, with indented sides. Gametangial cysts, embedded in lime, are 60–100 µm diam and number 100–200(–300) per ray. Algae are green in color with whitish stalks.

*Habitat and Comments:* *Acetabularia schenckii* grows attached to stones, rubble, coral fragments, or shells in the intertidal and shallow waters of protected habitats, mostly 1–2 m depths. The species has also reportedly been dredged off the Dry Tortugas to 73.2 m depths (Taylor 1928). Although Solms-Laubach (1895) concluded that *A. schenckii* was a living member of the genus *Acicularia*, the species has, nevertheless, been treated as member of *Acetabularia* (e.g., Egerod 1952; Valet 1969; Bailey et al. 1976; Berger et al. 2003; Guiry and Guiry 2022). [Illustrations: Børgesen 1908: figs. 8, 9; Bailey et al. 1976: figs. 1, 4, 6–9; Berger and Kaeffer 1992: fig. 3.72a–f; Berger 2006: figs. 193–207, 314; Littler et al. 2008: 236; Moura et al. 2014: figs. 4A–I.]

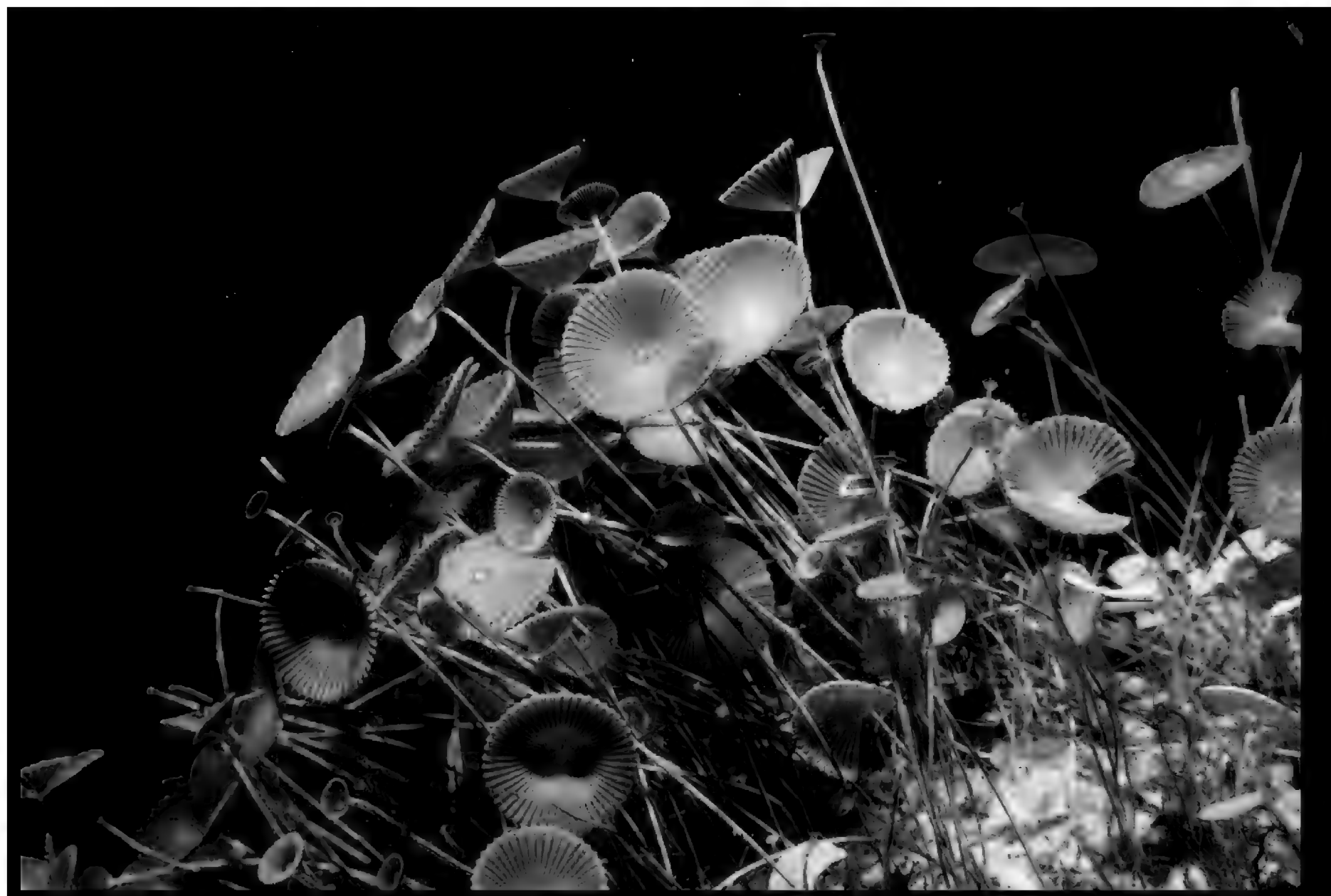


FIGURE 109. *Acetabularia crenulata*. In situ habit photograph from leeward Guayacan Island, La Parguera, 0.5 m. Field = approximately 8.0 cm.

**Parvocaulis S. Berger, Fettweiss, Gleissberg, Liddle, U. Richt., Sawitzky, et Zuccarello**

*Parvocaulis* S. Berger, Fettweiss, Gleissberg, Liddle, U. Richt., Sawitzky, et Zuccarello 2003: 559.

KEY TO THE *PARVOCAULIS* SPECIES OF PUERTO RICO

1. Stipes 1.0–3.0 mm tall; terminal cap 1.0–2.5 mm diam; gametangial cysts measure 68–72  $\mu\text{m}$  diam . . . . . *P. pusillus*  
 Stipes 5.0–10 mm tall; terminal caps 1.5–5.0 mm diam; gametangial cysts measure 90  $\mu\text{m}$  diam . . . . . *P. polyphysoides*

**Parvocaulis polyphysoides (P. Crouan et H. Crouan in Schramm and Mazé) S. Berger, Fettweiss, Gleissberg, Liddle, U. Richt., Sawitzky, et Zuccarello ex J. Norris et D. L. Ballant.**

*Parvocaulis polyphysoides* (P. Crouan et H. Crouan in Schramm and Mazé) S. Berger, Fettweiss, Gleissberg, Liddle, U. Richt., Sawitzky, et Zuccarello, ex J. Norris et D. L. Ballant. in Ballantine et al. 2023 [herein].

*Basionym*: *Acetabularia polyphysoides* P. Crouan et H. Crouan in Schramm and Mazé 1865: 42.

*Homotypic Synonyms*: *Polyphysa polyphysoides* (P. Crouan et H. Crouan) Schnetter 1978: 136, pl. 15N,O; *Parvocaulis polyphysoides* (P. Crouan et H. Crouan in Schramm and Mazé 1865: 42) S. Berger, Fettweiss, Gleissberg, Liddle, U. Richt., Sawitzky, et Zuccarello 2003: 559, comb. inval.\*

\* An incorrect basionym was cited by Berger et al. (2003: 559), thus making it invalid. Here a new combination proposal acknowledges the original authors and gives full and direct reference to place of publication, date, and page of the correct basionym (Turland et al., 2018: International Code of Botanical Nomenclature, Article 41.5).

*Puerto Rican Records*: As *Acetabularia polyphysoides*: Ballantine and Aponte 1997a, 2002. As *Polyphysa polyphysoides*: Hinds and Ballantine 1987.

*Western Atlantic Distribution*: Belize, Costa Rica, Panama, Mexico, Bermuda, Bahamas, Cuba, Guadeloupe, Jamaica, Puerto Rico. St. Eustatius.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Guadeloupe, French West Indies.

Thalli are solitary, 1.0–3.0(–10) mm tall. Stalks are 300–500  $\mu\text{m}$  diam and bear an umbrella-shaped terminal cap, 1.5–5.0 mm diam. The cap is composed of 11–25 obovoid to filiform, partially adherent rays. The rays measure 0.5–0.75 mm diam and are to 2.0 mm long. Ray end walls are rounded and barely apiculate. Fertile rays contain 6–50 gametangial cysts, each (25–)90  $\mu\text{m}$  diam. The corona superior possesses projecting knobs with an oval upper surface that bears 6–13 hairs or hair scars. A corona inferior is absent.

*Habitat and Comments*: *Parvocaulis polyphysoides* specimens are inconspicuous, and although not common, the species has been collected as a member of shallow-water coral reef turfs. Littler and Littler (2000) retained the species in *Acetabularia*. [Illustrations:

Axial cells are uninucleate and slender and possess annular wall thickenings. Thalli are calcified. The terminal caps are composed of ovate rays that are not laterally coherent; a corona inferior is absent. Two of the six recognized *Parvocaulis* species are known from Puerto Rico.

as *Acetabularia polyphysoides*, Vickers 1908: pl. 47; as *Polyphysa polyphysoides*, Berger and Kaever 1992: fig. 3.81a,b; as *Parvocaulis polyphysoides*, Berger et al. 2003: 559, figs. 12, 26.]

**Parvocaulis pusillus (M. Howe) S. Berger, Fettweiss, Gleissberg, Liddle, U. Richt., Sawitzky, et Zuccarello**

*Parvocaulis pusillus* (M. Howe) S. Berger, Fettweiss, Gleissberg, Liddle, U. Richt., Sawitzky, et Zuccarello 2003: 560, figs. 15, 29, 35.

*Basionym*: *Acetabulum pusillum* M. Howe 1909: 89, pl. 6: figs. 13–15, pl. 7: figs. 1–4.

*Homotypic Synonym*: *Acetabularia pusilla* (M. Howe) Collins 1909b: 379.

*Puerto Rican Records*: As *Parvocaulis pusillus*: Ballantine et al. 2016. As *Acetabularia pusilla*: Diaz-Piferrer 1963; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution*: Panama, North America, Bahamas, Cuba, Jamaica, Puerto Rico, Brazil, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Montego Bay, Jamaica.

The small thalli are solitary, possessing an unbranched, terete, and annulate stalk, (0.5–)1.0–2.0 mm long and 130–250  $\mu\text{m}$  diam. The stalks are attached to the substratum by digitate basal lobes. They bear a nearly flat terminal cap, 1.0–1.6 mm diam, composed of 6–11(–18) free (not adherent), ovoid to clavate rays. The rays have smooth, rounded apices, measuring 400–600  $\mu\text{m}$  long and 80.0–110.0  $\mu\text{m}$  diam at the base and 180–260  $\mu\text{m}$  diam distally. Corona superiors at the base of rays are small, cylindrical, ~25–50  $\mu\text{m}$  diam, and bear 2(–3) hairs. A corona inferior is absent. Each fertile ray produces 15–30 noncalcified, spherical gametangial cysts, 60–100  $\mu\text{m}$  diam. Algae are green in color, and the stalks are whitish.

*Habitat and Comments*: Noted as the smallest member of the genus (Berger et al. 2003), *Parvocaulis pusillus* is inconspicuous and easily overlooked. In Puerto Rico it occurs in shallow-water algal turf communities on reefs and in tide pools and subtidally on coral fragments and rubble and in crevices on the insular shelf offshore of La Parguera, at 40–49 m depths (Ballantine et al. 2016). [Illustrations: as *Acetabularia pusilla*, Littler and Littler 2000: 445; as *Parvocaulis pusillus*, Berger and Kaever 1992: fig. 3.87a,b; Berger 2006: figs. 267–279; Moura et al. 2014: fig. 8A–F.]



## ULOTRICHALES BORZI

### GAYRALIACEAE K. L. VINOGR.

*Notes:* A monotypic family, the genus *Gayralia* is similar morphologically to *Monostroma* Thuret (1854) and *Ulvaria* Ruprecht (1850) of the Ulvales. Molecular analyses of Hayden and Waaland (2002) supported generic separation of *Gayralia* and found the Gayraliaceae to belong in the Ulotrichales.

#### *Gayralia* K. L. Vinogr.

*Gayralia* K. L. Vinogr. 1969: 1354.

*Gayralia* thalli are initially saccate, later splitting or torn open to form simple monostromatic blades, varying from 1.0 to 100 cm in length. Blades are entire or torn with undulate margins and are attached to substratum by holdfast rhizoidal protuberances, or plants are unattached and free-floating. Cells in upper portion of the blade are polygonal and isodiametric, becoming more elongate proximally. Cells are uninucleate, possessing a single platelike chromatophore with a single prominent pyrenoid. Two species of the genus are recognized, one of which is known from Puerto Rico.

#### ***Gayralia oxysperma* (Kütz.) K. L. Vinogr. ex Scagel, P. W. Gabrielson, Garbary, Golden, M. W. Hawkes, S. C. Lindstrom, J. C. Oliveira, et Widd.**

*Gayralia oxysperma* (Kütz.) K. L. Vinogr. ex Scagel, P. W. Gabrielson, Garbary, Golden, M. W. Hawkes, S. C. Lindstrom, J. C. Oliveira, et Widd. 1989: 72.

*Basionym:* *Ulva oxysperma* Kütz. 1843: 296.

*Homotypic Synonyms:* *Ulvaria oxysperma* (Kütz.) Bliding 1969: 585, figs. 31A–F, 32A–J, 33; *Monostroma oxyspermum* (Kütz.) Doty 1947: 12.

*Puerto Rican Records:* As *Gayralia oxysperma*: Ballantine et al. 2016.

*Western Atlantic Distribution:* North America, Bermuda, Bahamas, Cuba, Puerto Rico, Trinidad and Tobago, Brazil, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Baltic Sea, Germany.

*Gayralia oxysperma* is the generitype. Thalli are very soft and delicate, at first saccate, then opening to form monostromatic, lanceolate to orbicular or sheetlike, simple to undulate blades, 1.0–2.0(–60) cm in height, 20–40(–60) µm thick. Algae are attached to the substratum by rhizoids from basal cells, or plants may become unattached and free-floating. Cells with thick walls are round to oval in vertical section, 15–40 µm tall, irregularly arranged, 7–18 µm diam in surface view. Algae are translucent light green in color.

*Habitat and Comments:* Typically, plants are found in shallow water, growing on mangrove roots and hard substrata in calm water. The Puerto Rican record is based on a few very small specimens that were collected at the edge of the Puerto Rican insular shelf to 65 m depth (Ballantine et al. 2016). It has also been found in deep water of Bermuda at 49–60 m depths (Frederick 1963). [Illustrations: Littler et al. 2008: 176; Cormaci et al. 2014: FP67, figs. 5–8; as *Ulvaria oxysperma*, Bliding 1969: figs. 31A–F, 32A–J, 33.]

### GOMONTIACEAE DE TONI

#### *Gomontia* Bornet et Flahault

*Gomontia* Bornet et Flahault 1888: 164.

Thalli are heteromorphic. Gametophytes form uniseriate irregularly branched filaments in tufts. They are partly endophytic, with basal creeping branched filaments or sometimes forming pseudoparenchymatous discs with downward growing rhizoids that penetrate shells, limestone, wood, or artificial substrata. Cells are cylindrical, ovoid, or polygonal with stratified cell walls and multinucleate with a single parietal, reticulate, or lobed chloroplast and several pyrenoids. Sexual reproduction is by biflagellate gametes. Sporophytes are a single cell, cylindrical, ovoid, or polygonal, and usually with a thickened cell wall. Asexual reproduction is by bi- or quadriflagellate zoospores released through exit tubes, aplanospores, and akinetes. There are eight currently recognized species of *Gomontia*. Of the two recorded in the western Atlantic, one is known to occur in Puerto Rico.

#### ***Gomontia polyrhiza* (Lagerh.) Bornet et Flahault**

*Gomontia polyrhiza* (Lagerh.) Bornet et Flahault 1888: 163.

*Basionym:* *Codiolum polyrhizum* Lagerh. 1886: 22, pl. 28, figs. 1–6.

*Puerto Rican Records:* As *Gomontia polyrhiza*: Almodóvar and Blomquist 1965; Almodóvar et al. 1979; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Mexico, North America, Bermuda, Bahamas, Jamaica, Netherlands Antilles, Puerto Rico, U.S. Virgin Islands, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Near Kristineberg, Sweden.

*Gomontia polyrhiza* is the generitype species. Algae are endophytic in limestone or shells. Thalli are composed of branched filaments with cells 4.0–8.0 µm diam and up to 50 µm long. Sporangia are produced at the surface and measure 30–40 µm diam and 150–250 µm long.

**Habitat and Comments:** *Gomontia polyrhiza* is commonly found in shells in shallow and intertidal habitats, giving the substratum a greenish cast. O’Kelly et al. (2004b) commented on molecular studies that showed several shell-boring, similar-looking *Codiolum*-like/*Gomontia polyrhiza*-like phases were involved in heteromorphic life histories of other algae, for example, *Ulvopsis*, *Eugomontia*, and *Entocladia*. Thus, molecular and life history studies of Puerto Rican *G. polyrhiza* are needed to verify its taxonomic identification. [Illustrations: Kylin 1949: fig. 7; Nielsen and Correa 1987: figs. 1–9; Cormaci et al. 2014: FP73, fig. 1.]

## ULVALES BLAKMAN ET TANSLEY

### BOLBOCOLEONACEAE O’KELLY ET RINKEL

**Note.** On the basis of genetic analyses, O’Kelly et al. (2004a) indicated that *Bolbocoleon piliferum* represented a distinct lineage basal to the Ulvales separate from Ulvaceae and Ulvellaceae and described the new family, Bolbocoleonaceae O’Kelly et Rinkel, in Brodie et al. (2007).

#### ***Bolbocoleon* Pringsh.**

*Bolbocoleon* Pringsh. 1863:2.

Thalli are mostly prostrate, epi- and/or endophytic, of irregularly, alternately branched uniseriate filaments. Cells are irregularly cylindrical, swollen, or developing protuberances and contain a parietal lobed chloroplast with several pyrenoids. One of the two recognized *Bolbocoleon* is known from Puerto Rico.

#### ***Bolbocoleon piliferum* Pringsh.**

FIGURE 110

*Bolbocoleon piliferum* Pringsh. 1862: 2, 8, pl. 1, figs. 1–6.

**Puerto Rican Record:** Ballantine et al. 2015.

**Western Atlantic Distribution:** North America, Netherlands Antilles, Puerto Rico, Brazil.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Helgoland, Germany.

*Bolbocoleon piliferum* is the generitype species. Thalli are epi-endophytic, composed of elaborate networks of mostly prostrate filaments, 4.0–6.0 µm in diameter, that grow out from irregularly enlarged, bulbous cells up to 30 µm in length and up to 20 µm diam. Cells typically have setae, although they are not always present.

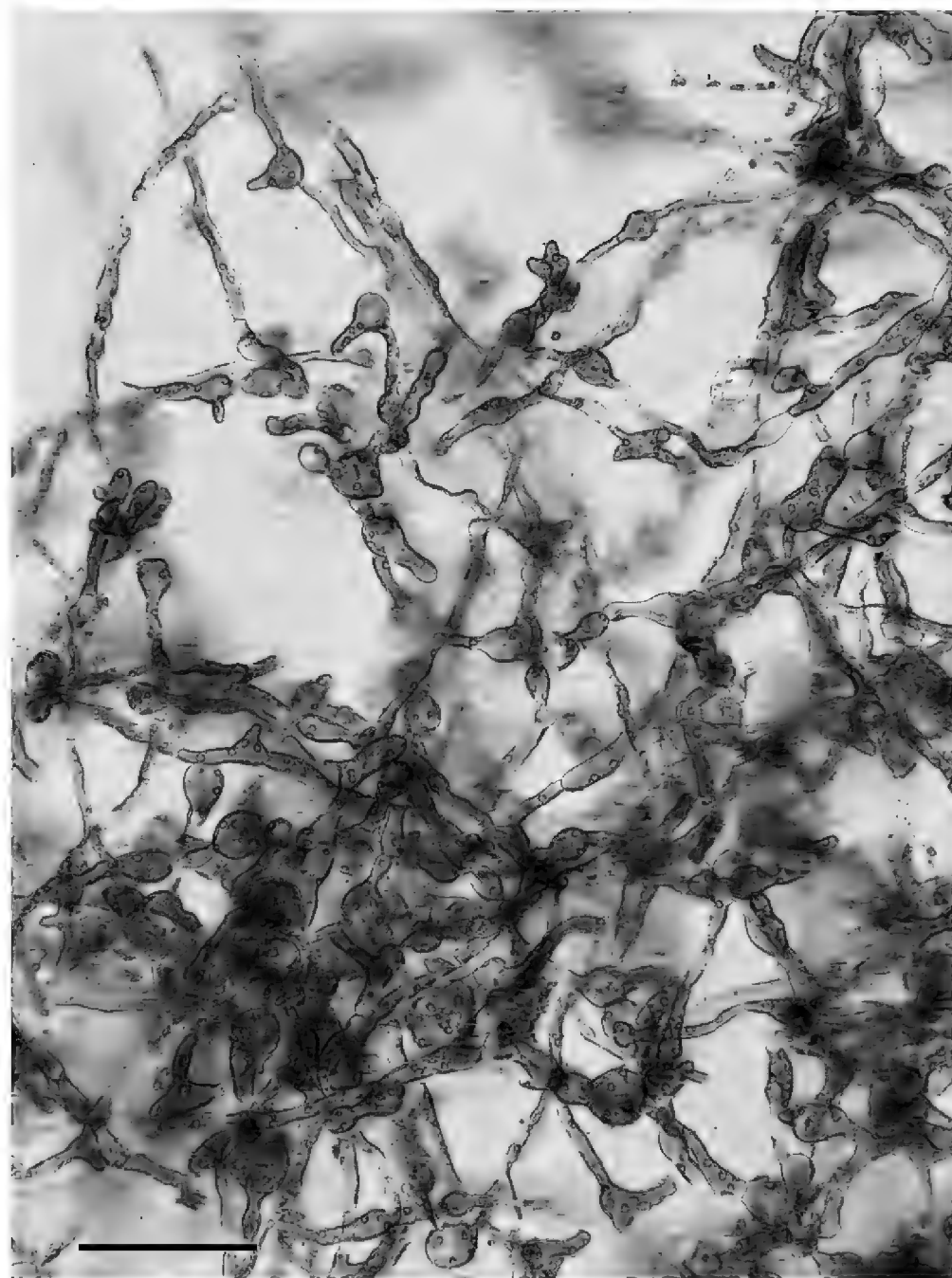


FIGURE 110. *Bolbocoleon piliferum*. DLB8425: Photomicrograph of cultured algae epiphytic on *Acanthophora spicifera* (Vahl) Børgesen, collected on *Rhizophora* roots, Enrique Reef, La Parguera. Scale bar = 500 µm.

**Habitat and Comments:** In Puerto Rico, *Bolbocoleon piliferum* first appeared as a contaminant in cultures of locally field collected *Acanthophora spicifera* (M. Vahl) Børgesen. [Additional illustrations: Cormaci et al. 2014: FP87, figs. 1–2.]

## PHAEOPHILACEAE CHAPPELL, O’KELLY, L. W. WILCOX, ET G. L. FLOYD

### ***Phaeophila* Hauck**

*Phaeophila* Hauck 1876: 56.

Thalli are epi- or endophytic with irregular laterally branched uniseriate filaments. Rounded to cylindrical cells possess irregular swellings and 1–3 long hairs without basal cross walls. Cells have lobed parietal chromatophores with several

pyrenoids. Nine species of *Phaeophila* are currently recognized; one of these is known from Puerto Rico.

***Phaeophila dendroides* (P. Crouan et H. Crouan) Batters**

*Phaeophila dendroides* (P. Crouan et H. Crouan) Batters 1902: 13.

*Basionym*: *Ochlochaete dendroides* P. Crouan et H. Crouan 1852: no. 346.

*Heterotypic Synonym*: *Phaeophila floridearum* Hauck 1876: 56, fig. p. 57.

*Puerto Rican Records*: As *Phaeophila dendroides*: Ballantine 1977; Almodóvar et al. 1979; Almodóvar and Ballantine 1983, Ballantine and Aponte 1997a; Ballantine et al. 2001; Ballantine and Aponte 2002; Ballantine et al. 2016.

*Western Atlantic Distribution*: Mexico, North America, Bermuda, Hispaniola, Jamaica, Netherlands Antilles, Puerto Rico, U.S. Virgin Islands, Brazil, Venezuela.

*World Distribution*: See Guiry and Guiry (2022).

*Type Locality*: Brest, Finistère, France.

Thalli are microscopic, composed of many irregular, laterally branched prostrate filaments. Cells are mostly cylindrical or irregular, some may be swollen, 9.0–40 µm diam and 15–50(–80) µm long, with a parietal chloroplast and 1–13 pyrenoids, bearing 1–3 colorless hairs (setae), often spirally twisted and lacking basal cross walls.

*Habitat and Comments*: *Phaeophila dendroides* is common in Puerto Rico, occurring in mostly shallow-water habitats as epiphytes on seagrasses and other algae as well as in or on mollusk or barnacle shells, crustose corallines, and other limestone substrata and subtidally at the edge of the insular shelf off Guánica at 65 m depth (Ballantine et al. 2016). [Illustrations: as *Phaeophila floridearum*, Hauck 1876: 56, fig. 11; as *Phaeophila dendroides*,

O’Kelly and Yarish 1981: figs. 1, 15–27; Nielsen 1987: figs. 9C–E, 10; Brodie et al. 2007: fig. 29; Cormaci et al. 2014: 96FP, fig. 1.]

**ULVACEAE LAMOUROUX EX DUMORTIER**

***Ulva* L.**

*Ulva* L. 1753: 1163, nom. et typ. cons.

*Synonym*: *Enteromorpha* Link 1820: 5. nom. et typ. cons.

*Ulva* thalli are either bladelike or tubular, encompassing two previously recognized genera, *Enteromorpha* and *Ulva* sensu Taylor 1960. When bladelike, thalli are crispate, orbicular, lobed, or elongate laciniate and 2 cells thick. Tubular species are a single layer thick. There are 8 species of *Ulva* known for Puerto Rico and 148 recognized species worldwide. They are members of two taxonomic sections (secto) of *Ulva* based on their morphologies.

*Notes*: The genus *Ulva* L. (1753) was considered to be a single genus until Link (1820) recognized *Enteromorpha*. It had been long recognized that *Enteromorpha* and *Ulva* are closely related, and more recent molecular analyses have supported the Linnean concept that *Ulva* and *Enteromorpha* constitute a single genus (Tan et al. 1999; Shimada et al. 2003; Hayden et al. 2003). Regarding the nomenclature of the species, Brodie et al. (2007) and O’Kelly et al. (2010) have suggested species of *Ulva* in tropical and subtropical regions are mostly unique to these areas and different from types from Europe. Therefore, the tropical-subtropical species identified with type species of boreal Europe and North America are likely incorrectly identified and probably represent different species. Humm and Taylor (1961) have pointed out the high degree of difficulty in *Enteromorpha* taxonomy.

**KEY TO THE *ULVA* SPECIES OF PUERTO RICO**

1. Thalli membranous, 2 cells thick when viewed in section ..... 2 (*Ulva* sect. *Ulva*)  
Thalli tubelike, 1 cell thick when viewed in section ..... 4 (*Ulva* sect. *Enteromorpha*)
2. Thalli divided into narrow segments ..... *U. lactuca*  
Thalli simple or broadly lobed ..... 3
3. Holdfast small; in section cells of older parts are nearly square or slightly taller than broad ..... *U. cf. fenestrata*  
Holdfast distinct; in section cells of older parts are taller than broad ..... *U. lacunculata*
4. Generally 1–3 cell cells when viewed in section ..... *U. chaetomorphoides*  
Plants tubular ..... 5
5. Plants simple or subsimple ..... 6  
Plants usually branched ..... 7
6. Plants with cells in longitudinal series, at least below; cells 10–28 µm diam ..... *U. flexuosa*  
Cells 9–15 µm diam ..... *U. intestinalis*
7. Cells in marked longitudinal rows ..... *U. clathrata*  
Cells not in longitudinal rows ..... *U. compressa*

***Ulva* sect. *Ulva***

Members of *Ulva* sect. *Ulva* are species that are flat, blade-like, and distromatic throughout (in section). Three species of *Ulva* in this section occur in Puerto Rico.

***Ulva* cf. *fenestrata* Postels et Ruprecht**

FIGURE 111

*Ulva* cf. *fenestrata* Postels et Ruprecht 1840: 21, pl. 37.

*Synonym:* *Ulva lactuca* sensu Taylor 1960: 65.

*Puerto Rican Records:* As *Ulva lactuca*: Almodóvar and Blomquist 1959, 1961; Taylor 1960; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997a, 2002.

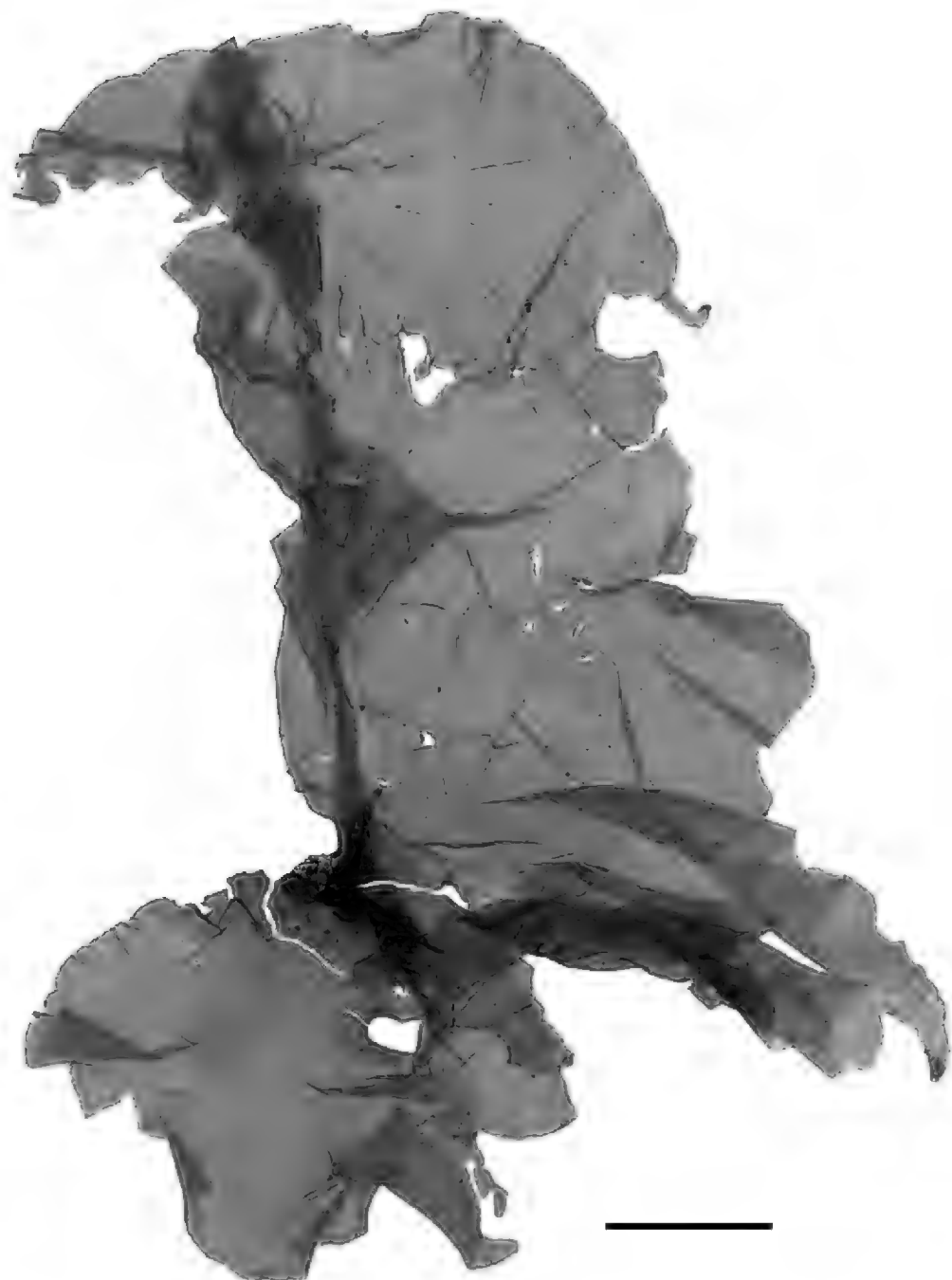
*Western Atlantic Distribution:* As *Ulva lactuca*: Belize, Costa Rica, Panama, North America, Bermuda, Bahamas, Barbados, Cayman Islands, Cuba, Dominica, Grenadines, Guadeloupe, Hispaniola, Jamaica, Antigua, Martinique, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Uruguay, Venezuela, Argentina.

*World Distribution:* As *Ulva lactuca*: see Guiry and Guiry (2022).

*Type Locality:* Kamchatka, Russian Federation, fide Hughey et al. (2019).

Thalli consist of thin sheets originating from small hold-fasts, reaching 10–100 cm or more long and to 70 cm broad. Plants are attached by rhizoids forming a small discoid hold-fast. Sheets are variable in shape, lanceolate to rounded, often lobed and undulate with entire or ruffled margins. In section, the sheets are 2 cells and 50–90(–120)  $\mu\text{m}$  thick. Cells, with a parietal chloroplast and 1–2 pyrenoids, are rectangular or irregularly polygonal, sometimes arranged in pairs, measuring 8.0–12  $\mu\text{m}$  wide and 12–14  $\mu\text{m}$  long in surface view. Algae are light to dark green in color.

*Habitat and Comments:* “*Ulva lactuca*,” as it has usually been referred to in Puerto Rico, is probably not that species and is herein referred to *U. cf. fenestrata*. The Puerto Rican taxon is generally found in calm waters to 10 m depth, often in areas with elevated nutrient input, and may be found attached or frequently encountered unattached and drifting. Hughey et al. (2019) showed that the cold temperate and Pacific species that had been referred to *Ulva lactuca* L. was *U. fenestrata* on the basis of *rbcL* sequence analysis of a voucher from the holotype locality. Melton and Lopez-Bautista (2021), in their molecular examination of *Ulva* species from the Gulf of Mexico and the U.S. east coast, subsequently found multiple sheetlike species that superficially resemble “*Ulva lactuca*,” including *U. fenestrata*. We remain somewhat skeptical as to the proper identity of Puerto Rican material until genetic comparisons can be made. [Additional illustrations: as *Ulva lactuca*, Vickers 1908: pl. 1; Littler et al. 2008: 185; as *Ulva fenestrata*, Melton and Lopez-Bautista 2021: fig. 4D.]



**FIGURE 111.** *Ulva* cf. *fenestrata*. LRA6142, herbarium specimen: Cayo Palomas, Tallaboa Bay, Guayanilla. Scale bar = 2.0 cm.

***Ulva lacinulata* (Kütz.) Wittrock**

*Ulva lacinulata* (Kütz.) Wittrock 1882: 433.

*Basionym:* *Phycoseris lacinulata* Kütz. 1847: 165.

*Synonyms:* *Ulva lactuca* var. *lacinulata* (Kütz.) W. R. Taylor 1960: 65; *Ulva rigida* sensu Ballantine and Norris 1989; Ballantine and Aponte 1997a, 2002 [non *Ulva rigida* C. Agardh 1823: 410]; *Ulva lactuca* var. *rigida* sensu Almodóvar 1962 [non *Ulva lactuca* var. *rigida* (C. Agardh) Le Jolis 1863: 38].

*Puerto Rican Records:* As *Ulva rigida*: Ballantine and Norris 1989; Ballantine and Aponte 1997a, 2002. As *Ulva lactuca* var. *rigida*: Almodóvar 1962.

*Western Atlantic Distribution:* Belize, Costa Rica, North America, Bermuda, Antigua, Barbados, Cayman Islands, Cuba, Dominica, Grenadines, Netherlands Antilles, Puerto Rico, Brazil, Colombia, Venezuela, Argentina.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Hvara, Croatia.



Thalli are sheetlike blades derived from a distinct holdfast and stalk. The texture is firm to rigid in low to mid portions and less so distally. Blades are variable in shape, being strap shaped to possessing broad lobes. The blades measure (5–)10(–100) cm long and 40–60  $\mu\text{m}$  thick proximally, increasing to 110–200  $\mu\text{m}$  thick distally. The surface is entire or with few to many holes, and the blade margins are irregularly dentate. Cells in surface view are polygonal to rectangular with rounded corners, 12–15  $\mu\text{m}$  tall and 13–15  $\mu\text{m}$  wide in upper portions of blade. Cells have a single chloroplast with (1–)2(–3) pyrenoids. Algae are pale, dark, or bright green in color.

*Habitat and Comments:* *Ulva lacinulata* occurs in exposed to protected habitats of the intertidal and shallow water to 2.0 m depths and may be attached on limestone, rocks, mangrove prop roots, and other hard surfaces or sometimes unattached and in the drift. Puerto Rican specimens previously referred to *U. rigida* are now recognized as *U. lacinulata*, following Hughey et al. (2021), who reinstated *Ulva lacinulata* and indicated the distribution of *U. rigida* was limited to Europe. [Illustration: as *U. rigida*, Littler et al. 2008: 189.]

### ***Ulva lactuca* L.**

FIGURE 112

*Ulva lactuca* L. 1753: 1163.

*Synonym:* *Ulva fasciata* sensu Taylor 1960: 66, pl. 1: fig. 4. [non Delile 1813: 297, pl. 58: fig. 5].

*Puerto Rican Records:* As *Ulva fasciata*: Taylor 1960; Almodóvar 1964a, 1964b; Almodóvar and Ballantine 1983; Ballantine and Aponte 2002.

*Western Atlantic Distribution:* Belize, Costa Rica, Mexico, North America, Bermuda, Antigua, Cuba, Dominica, Guadeloupe, Grenadines, Hispaniola, Honduras, Jamaica, Martinique, Netherlands Antilles, Nevis, Puerto Rico, St. Barthélemy, St. Kitts, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Uruguay, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* “In Oceano” (Linnaeus 1753: 1163) or possibly “Indo-Pacific” (see Hughey et al. 2019).

Thalli are thin sheetlike blades, up to 100  $\mu\text{m}$  thick and 10–75(–150) cm in length, that expand and usually irregularly divide into long linear segments, 0.5–5.0 cm wide. Blades have a cuneate base above a short stalk with a very small holdfast and margins that are entire and often irregularly ruffled. Cells measure 8.0–20  $\mu\text{m}$  wide and 14–40  $\mu\text{m}$  long, being taller than broad in section. Algae are bright green in color.

*Habitat and Comments:* *Ulva lactuca* is typically in areas with increased nutrient enrichment and may reach up to 75

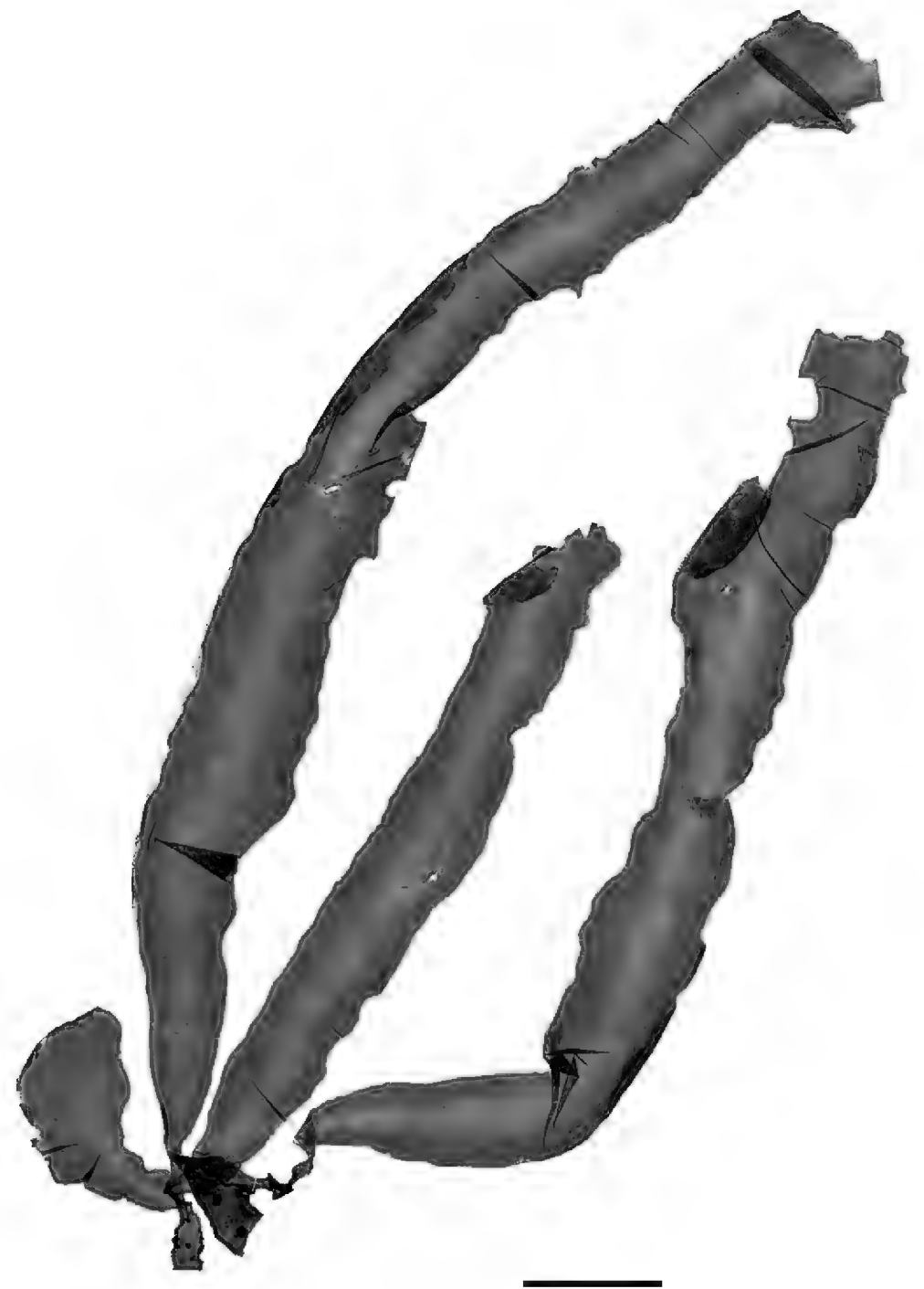


FIGURE 112. *Ulva lactuca*. LRA7133, herbarium specimen: Bird Island, La Parguera. Scale bar = 2.0 cm.

cm in length. Large growths of *U. lactuca* have been observed growing on *Rhizophora* prop roots on “Bird Island” (so named because it was an egret rookery), located just west of Magueyes Island. Previously known as “*Ulva fasciata*” in Puerto Rico, O’Kelly et al. (2010) have treated *U. fasciata* as a synonym of *U. lactuca*, and Hughey et al. (2019) concluded the two were synonyms on the basis of their genetic analyses of an epitype of *U. fasciata* (type locality: New Port, Alexandria, Egypt; Delile 1813: 297). The type locality of *U. lactuca* is uncertain; originally given as “in oceano” (Linnaeus 1753), it has generally been assumed to be Europe or the western coast of Sweden (e.g., Womersley 1984) or “Atlantic Ocean” (Guiry and Guiry 2022), but Hughey et al. (2019) noted it was possibly “Indo-Pacific.” [Additional illustrations: as *Ulva fasciata*, Vickers 1908: pl. 2; Taylor 1960: pl. 1: fig. 4; Littler et al. 2008: 182; as *Ulva lactuca*, Melton and Lopez-Bautista 2021: fig. 4E.]

***Ulva* sect. *Chaetomorphoides* J. N. Norris et  
D. L. Ballantine sect. nov.**

*Type Species: Ulva chaetomorphoides* (Børgesen) H. S. Hayden et al. 2003: 288.

Members of *U.* sect. *Chaetomorphoides* are filiform, cylindrical, and simple to branched species of *Ulva* that are mostly 1–3 cells thick (solid in section), less commonly with portions of 4 or more cells (hollow in cross section) and branches ending in single row of cells.

***Ulva chaetomorphoides* (Børgesen) H. S. Hayden,  
Blomster, Maggs, P. C. Silva, Stanhope, et Waaland**

*Ulva chaetomorphoides* (Børgesen) H. S. Hayden, Blomster, Maggs, P. C. Silva, Stanhope, et Waaland 2003: 288, table 4.

*Basionym: Enteromorpha chaetomorphoides* Børgesen 1911: 149, Fig. 12.

*Puerto Rican Records:* As *Enteromorpha chaetomorphoides*: Taylor 1960; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Belize, Costa Rica, North America, Bermuda, Barbados, Cuba, Jamaica, Martinique, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Bovoni Lagoon, St. Thomas, U.S. Virgin Islands.

Thalli are thin, cylindrical, and simple to sparsely to abundantly branched, consisting of 1–3 (rarely 4 or more) cells in longitudinal rows up to 60 µm diam. Attachment is by a 2–3-celled basal portion that produces rhizoids. Primary axes are composed generally of 2–3 cells (solid in section), measuring 45 µm diam, and rarely wider than 4 or more cells (when hollow). Branches are composed of (2–) mostly 3 rows of cells, terminating in a single row of cells. Cells are subquadrate to rectangular, 15–18 µm diam, with parietal chloroplasts containing 2–3 pyrenoids. Algae are bright green in color.

*Habitat and Comments:* *Ulva chaetomorphoides* is often unattached, forming loose, entangled masses in protected shallow-water habitats of mangroves or lagoons. It also may be entangled with or occasionally epiphytic on mangrove prop roots or other algae down to 10 m depths. [Illustrations: Børgesen 1911: fig. 12, 1913: fig. 1a–f; Schneider and Lane 2005: figs. 1–3; Littler et al. 2008: 139.]

***Ulva* sect. *Enteromorpha* (Link) Endlicher**

*Ulva* sect. *Enteromorpha* (Link) Endlicher 1843: 19.

*Basionym: Enteromorpha* Link 1820: 5, [2, index].

Most members of *U.* sect. *Enteromorpha* are tubular to compressed and completely monostromatic. Four species of this section are known in Puerto Rico.

***Ulva clathrata* (Roth) C. Agardh**

*Ulva clathrata* (Roth) C. Agardh 1811: 23.

*Basionym: Conferva clathrata* Roth 1806: 175.

*Homotypic Synonym: Enteromorpha clathrata* (Roth) Grev. 1830: lxvi, 181.

*Puerto Rican Records:* As *Enteromorpha clathrata*: Taylor 1960; Almodóvar 1964a; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* Belize, Mexico, North America, Bermuda, Cuba, Dominica, Grenadines, Guadeloupe, Hispaniola, Netherlands Antilles, Nevis, Puerto Rico, U.S. Virgin Islands, Brazil, Argentina.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* Fehmarn (island off east coast of Schleswig-Holstein, northern Germany), SW Baltic Sea.

*Neotype Locality:* Baltic Øresund (strait off southern Sweden); type missing (Bliding 1963: 109); Herbarium Agardh 13737 (LD), pictured by Bliding (1963: 113, fig. 69a,b), was selected as a neotype by Blomster et al. (1999: 579); see also Hayden et al. (2003).

Cylindrical to slightly compressed, tubular thalli are repeatedly branched and form tufts to 10–15(–40) cm tall that are 250 µm to 0.5(–1.00) mm diam. Thalli possess abundant lateral spinelike branchlets that terminate in a single cell or in a uniseriate tip of 5 or more cells. Cells (in surface view) are in longitudinal rows, remaining ordered or becoming more randomly arranged in older portions. The cells are usually rectangular in shape, 12–36 µm long and 10–20(–50) µm diam. Cells possess a single chloroplast and 1 or more pyrenoids. Algae are light to dark green in color.

*Habitat and Comments:* In Puerto Rico *Ulva clathrata* is epiphytic on seagrasses or epilithic on stones and shells in intertidal to shallow-water protected to exposed habitats. Unattached *U. clathrata* can form floating masses, often in lagoons or marshes. Brodie et al. (2007) remarked that records identified as “*U. clathrata*” outside of Europe require reassessment. [Illustration: Littler et al. 2008: 180.]

***Ulva compressa* L.**

*Basionym: Ulva compressa* L. 1753: 1163.

*Homotypic Synonyms: Enteromorpha compressa* (L.) Nees 1820: Index 2;  
*Enteromorpha compressa* (L.) Grev. 1830: 180, comb. illeg.

*Puerto Rican Records:* As *Enteromorpha compressa*: Taylor 1960; Ballantine and Aponte 1997a, 2002.

*Western Atlantic Distribution:* North America, Bermuda, Barbados, Cuba, Grenadines, Guadeloupe, Martinique, Puerto Rico, St. Eustatius, Trinidad and Tobago, Brazil, Guyana, Uruguay, Venezuela, Argentina.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* “Habitat in Europae mari & tectis maritimis.”

*Lectotype Locality:* Probably Bognor, Sussex, England; based on selection of lectotype illustration of Dillenius (1742: pl. 9: fig. 8), cited by Linnaeus (1753), and topotype by Blomster et al. (1998: 332, figs. 50, 55–57). See also: Hayden et al. (2003).

Tubular thalli are compressed, not inflated, and measure to 10–30(–60) cm tall and 0.5–6.0 cm diam. Thalli are unbranched or occasionally with basal branches. Algae are generally tapered proximally and attenuate terminally, attached by rhizoidal hold-fasts. Cells in surface view are subquadrate, angular or rounded, 10–15(–18)  $\mu\text{m}$  diam, irregularly arranged. Cells contain a large chloroplast and 1 pyrenoid per cell. Algae are bright to dark green or yellowish in color.

*Habitat and Comments:* *Ulva compressa* occurs from the intertidal to 25 m depth, on rocks, coral rubble, shells, and piling. [Illustrations: Blomster et al. 1998: figs. 4–6, 35–40, 50, 55–57; Littler et al. 2008: 181.]

### ***Ulva flexuosa* Wulfen**

FIGURE 113

*Ulva flexuosa* Wulfen 1803: xxii, 1.

*Homotypic Synonyms:* *Enteromorpha flexuosa* (Wulfen) J. Agardh 1883: 126.

*Heterotypic Synonyms:* *Enteromorpha lingulata* J. Agardh 1883: 143; *Enteromorpha plumosa* Kütz. 1843: 300.

*Misapplied Name:* *Enteromorpha erecta* (Lyngbye) Carmich. in W. J. Hooker 1883: 314.

*Puerto Rican Records:* As *Enteromorpha flexuosa*: Almodóvar and Blomquist 1961; Almodóvar and Biebl 1962; Almodóvar 1964a; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine and Aponte 1997a, 2002. As *Enteromorpha erecta*: Diaz-Piferrer 1963. As *Enteromorpha lingulata*: Taylor 1960; Miller and Ballantine 1974; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine and Aponte 2002. As *Enteromorpha plumosa*: Taylor 1960; Almodóvar and Ballantine 1983.

*Western Atlantic Distribution:* Belize, Costa Rica, Mexico, Panama, North America, Bermuda, Bahamas, Barbados, Bequia, Cuba, Grenadines, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, St. Barthélemy, St. Eustatius, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Uruguay, Venezuela, Argentina.

*World Distribution:* See Guiry and Guiry (2022).

*Type Locality:* “Duini ad littoral maris Adriatici” (Wulfen 1803: [1]); Duino (NW of Trieste), Italy, Adriatic Sea (Womersley 1984).



FIGURE 113. *Ulva flexuosa*. DLBsn, herbarium specimen: Ballena Bay, Guánica. Scale bar = 1.0 cm.

Tubular to slightly compressed thalli, to 10(–25) cm tall and (1.0–)0.5–5.0(–10) mm diam, are attached basally by rhizoids. Thalli are unbranched or sparsely to abundantly branched with opposite and lateral branches about the same size as the main axes. Cells in surface view are in longitudinal and transverse rows (more evident in younger, narrow portions; less distinct in older, broader portions), and angular, quadrate to elongate, 9.0–20 µm long and 8–15 µm wide. Cells possess a single parietal chloroplast with 1–2 pyrenoids and thin to thick cell walls. In transverse section, cells are 20–30 µm thick, with cells 12–30 µm tall and 9–20 µm wide.

**Habitat and Comments:** *Ulva flexuosa* is typically found in shallow-water habitats on rocks, shells, coral rubble, and mangrove roots. The species is recognized to be highly variable in overall morphology. [Additional illustration: Vickers 1908: pl. 1; Littler et al. 2008: 183; Huisman 2015: fig. 3A,B.]

### ***Ulva intestinalis* L.**

*Ulva intestinalis* L. 1753: 1163.

**Homotypic Synonym:** *Enteromorpha intestinalis* (L.) Nees 1820: Index 2.

**Puerto Rican Records:** As *Enteromorpha intestinalis*: Taylor 1960; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

**Western Atlantic Distribution:** North America, Bermuda, Cuba, Grenadines, Guadeloupe, Jamaica, Netherlands Antilles, Puerto Rico, Brazil, Uruguay, Venezuela, Argentina.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** “In Mari omni” (Linnaeus 1753).

**Lectotype Locality:** Woolwich, River Thames, London, England; based on lectotype illustration of Dillenius (1742: pl. 9: fig. 7) selected by Blomster et al. (1999: 332).

Tubular thalli, (0.3–)30–50 cm tall and (1.0–)3–5 mm in diameter, are unbranched or relatively little branched. Plants

taper basally to a stalk-like portion, attached by rhizoids, or are unattached and free-floating. Thalli may be slightly compressed, becoming irregularly inflated, contorted, and constricted, measuring 0.5–6.0(–10) cm wide. Cells in surface view are rectangular, rounded, 5.0–12(–20) µm long and 5.0–10 µm wide, not in longitudinal rows. Cells possess thick cell walls and chloroplasts with 1(–2) pyrenoids. Algae are light to dark green in color.

**Habitat and Comments:** *Ulva intestinalis* occurs on rocks or rubble or is often free-floating or occasionally epiphytic on other algae in moderately exposed intertidal to shallow waters and lagoons. The *U. intestinalis* record from Puerto Rico may prove to be incorrect as Humm and Taylor (1961) considered the species to have cold-water affinities, being present in the Gulf of Mexico only in winter months. O’Kelly et al. (2010) also expressed the opinion that specimens referred to this epithet from tropical or subtropical locations were incorrect. The original record of *Ulva intestinalis* from Puerto Rico is by Taylor (1960); the subsequent reports have followed Taylor. [Illustrations: Bliding 1963: figs. 87a–g, 88a–b; Blomster et al. 1998: figs. 49 (topotype), 52–54; Littler et al. 2008: 184; Braune and Guiry 2011: fig. 2.1.]

### **ULVELLACEAE SCHMIDLE**

#### ***Ulvella* P. Crouan et H. Crouan**

*Ulvella* P. Crouan et H. Crouan 1859: 288.

*Ulvella* possesses thalli with free filaments or filaments partially coalesced to form epiphytic, endophytic, or lithophytic discs. Cells possess a parietal chromatophore and lack pyrenoids. When disclike in morphology, cells in the center are arranged irregularly and in more than 1 layer. Marginal filamentous cells are unistratose and have forked apical cells. There are 3 *Ulvella* species in Puerto Rico, and a total of 51 recognized species.

### **KEY TO THE *ULVELLA* SPECIES OF PUERTO RICO**

1. Plants endophytic, growing within the cell membranes of other algae ..... *U. viridis*  
Plants epiphytic, not penetrating their basiphytes ..... 2
2. Plants filamentous throughout, congested in the center ..... *U. scutata*  
Plants discoid, marginally subfilamentous, discs more than 1 cell thick in the center .....  
..... *U. lens*

#### ***Ulvella lens* P. Crouan et H. Crouan**

FIGURE 114

*Ulvella lens* P. Crouan et H. Crouan, 1859: 288.

**Puerto Rican Records:** Diaz-Piferrer 1963; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

**Western Atlantic Distribution:** North America, Bermuda, Bahamas, Netherlands Antilles, Puerto Rico, U.S. Virgin Islands, Venezuela.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Brest, Finistère, France.

*Ulvella lens* is the generitype. Thalli measure to 0.4–5 mm diam. Irregularly placed cells in the central portion, 5–10(–25) µm diam, are several cells and 8–25 µm thick.





FIGURE 114. *Ulvella lens*. DLBsn, photomicrograph: Guajataca, intertidal, epiphytic on *Chaetomorpha* sp. Scale bar = 25  $\mu$ m.

Marginally oriented filaments measure 3.0–4.0(–15)  $\mu$ m broad and are 15–30  $\mu$ m long. Some cells are bifurcate at the margin.

**Habitat and Comments:** Algae are highly inconspicuous, growing on coarse algae and seagrasses, as epizootics, and on hard substratum. [Additional illustrations: Kylin 1949: fig. 48; Littler et al. 2008: 191; Cormaci et al. 2014: FP179, figs. 3–5.]

***Ulvella scutata* (Reinke) R. Nielsen, O’Kelly, et Wysor**

*Ulvella scutata* (Reinke) R. Nielsen, O’Kelly, et Wysor in Nielsen et al. 2013: 52.

**Basionym:** *Pringsheimia scutata* Reinke 1888: 241.

**Homotypic Synonym:** *Pringshiemiella scutata* (Reinke) Marchew. 1925: 42 (as *scuttata*).

**Puerto Rican Records:** As *Pringshiemiella scutata*: Ballantine and Norris 1989; Ballantine and Aponte 1997a, 2002.

**Western Atlantic Distribution:** Belize, North America, Bermuda, Jamaica, Netherlands Antilles, Puerto Rico, U.S. Virgin Islands, Brazil, Venezuela.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Near Kieler Bucht, Baltic Sea.

Thalli are monostromatic disks, 1.0–2.0 mm diam and 10–12  $\mu$ m thick, composed of radiating dichotomously branched coalescing filaments. The filament cells measure 5.0–25  $\mu$ m broad and 10–40  $\mu$ m long. Cells at the margin are bifurcate.

Central cells are columnar and measure to 140  $\mu$ m tall. Algae are bright green in color.

**Habitat and Comments:** Algae are epiphytic on coarse algae and seagrass leaves. Only a single specimen from Puerto Rico is known, collected intertidally and epiphytically on *Chaetomorpha*. [Illustrations: as *Pringsheimiella scutata*, Collins 1909a: fig. 95; Kylin 1949: fig. 46; Cormaci et al. 2014: FP189, figs. 1–3.]

***Ulvella viridis* (Reinke) R. Nielsen, O’Kelly, et Wysor**

*Ulvella viridis* (Reinke) R. Nielsen, O’Kelly, et Wysor in Nielsen et al. 2013: 53.

**Basionym:** *Entocladia viridis* Reinke 1879: 476.

**Puerto Rican Records:** As *Entocladia viridis*: Ballantine 1977.

As *Ulvella viridis*: Almodóvar et al. 1979; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997a, 2002.

**Western Atlantic Distribution:** North America, Bermuda, Bahamas, Puerto Rico, U.S. Virgin Islands, Brazil, Uruguay.

**World Distribution:** See Guiry and Guiry (2022).

**Type Locality:** Naples, Italy.

Thalli are microscopic, with branched uniseriate filaments that measure 3.0–6.0(–12)  $\mu$ m diam. The cells are variable in length, being 1–6 diameters long. Filament cells are often irregularly swollen and distorted.

**Habitat and Comments:** *Ulvella viridis* occur as inconspicuous epiphytes on other algae and seagrasses. [Illustration: as *Entocladia viridis*, Kylin 1949: fig. 39.]

**PRASINODERMATOPHYTA B. MARIN ET MELKONIAN**

See Li et al. 2020 (as Prasinodermophyta).

**PALMOPHYLLOPHYCEAE, LELIAERT, TRONHOLM, LEMIEUX, TURMEL, DEPRIEST, D. BHATTACHARYA, KAROL, FREDERICQ, ZECHMAN, ET LOPEZ-BAUTISTA**

**PALMOPHYLLALES ZECHMAN, VERBRUGGEN, LELIAERT, ASHWORTH, ET HANISAK**

**PALMOPHYLLACEAE ZECHMAN, VERBRUGGEN, LELIAERT, ASHWORTH, ET HANISAK**

***Verdigellas* D. L. Ballant. et J. N. Norris**

*Verdigellas* D. L. Ballant. et J. N. Norris 1994: 369.

Thalli are soft, gelatinous, and erect or spreading. Algae are irregularly to uniformly compressed or broadly expanded above 1 or more stipes. Within the common gelatinous matrix are numerous small, irregularly arranged, spherical cells. The cells are more densely placed near the surface. Cells are

uninucleate, with a single cup-shaped chloroplast, lacking pyrenoids, eyespots, pseudoflagella, and gelatinous stalks. The genus contains three species, all restricted to the tropical western Atlantic and mostly restricted to deepwater habitats.

Two of the four recognized *Verdigellas* species are known from Puerto Rico. *Verdigellas* represents a clade of ancient lineage within the Chlorophyta (Zechman et al. 2010; Leliaert et al. 2016).

KEY TO THE VERDIGELLAS SPECIES OF PUERTO RICO

- Plants peltate with numerous holdfasts . . . . . *V. peltata*  
 Plants bladelike and basally attached; margins fimbriate . . . . . *V. fimbriata*

***Verdigellas fimbriata* D. L. Ballant. et J. N. Norris**

FIGURE 115

*Verdigellas fimbriata* D. L. Ballant. et J. N. Norris 1994: 369, figs. 1–4.

*Puerto Rican Records:* Ballantine and Norris 1994; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution:* North America, Puerto Rico, Brazil.

*Type Locality:* Mona Island, Puerto Rico.

*Verdigellas fimbriata* is the generitype species. Thalli reach 9.0 cm tall. They are peltate when young and become flattened and broadly expanded to 11 mm in width. In mature thalli, compressed or terete branchlets are densely placed at the margin. Simple or irregular branching occurs mostly in a single plane originating at the margins, up to 4(–5) degrees and branchlets progressively become smaller; branchlets occasionally fuse. Structurally, algae are composed of coccoid cells, 5.0–10 µm diam, irregularly arranged in a soft gelatinous matrix. Vegetative cells are densely placed at the surface and are less dense inward. Cyanobacterial filaments are abundant among vegetative cells.

*Habitat and Comments:* *Verdigellas fimbriata* is uncommon and restricted to deepwater habitats in Puerto Rico, to a depth of 65 m.

***Verdigellas peltata* D. L. Ballant. et J. N. Norris**

FIGURE 116

*Verdigellas peltata* D. L. Ballant. et J. N. Norris 1994: 369, figs. 5–7.

*Puerto Rican Records:* Ballantine and Norris 1994; Ballantine and Aponte 1997a, 2002; Ballantine et al. 2016.

*Western Atlantic Distribution:* Bahamas, Bermuda, South America.

*Type Locality:* Mona Island, Puerto Rico.

Thalli form simple, peltate, feltlike, gelatinous cushions, attached by a discrete stipe or stipes and/or occasionally directly from portions of the ventral surface when in contact with the substratum. Larger specimens form numerous stipes, to 1.0 mm long with spreading portions measuring to 20 mm across. Algae are of somewhat uneven thickness, and the margins are frequently undulate. Structurally, the species is composed of spherical cells, 6.0–9.0



FIGURE 115. *Verdigellas fimbriata*. DLB3606, Line drawing of holotype specimen, dredged along south coast of Mona Island, 60 m. Scale bar = 1.0 cm.

µm diam. The coccoid cells are densely placed outwardly and less densely inwardly. Algae are bright green in color.

*Habitat and Comments:* Ballantine and Aponte (2003) collected the species to 122 m from a submersible in the Bahamas, and *Verdigellas peltata* has been collected to 100 m in Puerto Rico. Littler and Littler (2000) indicated a maximum depth of 157 m for the species. Although most collections are in water deeper than 50

m, Schneider et al. (2010) reported the species from 2.0 to 3.0 m in a shaded grotto in Bermuda. *Verdigellas peltata* bears superficial resemblance to another deepwater species, *Palmophyllum crassum* (Naccari) Rabenhorst, from Bermuda (Taylor 1960). *Palmophyllum* possesses cells with gelatinous stalks that are not possessed by *Verdigellas*. *Palmophyllum* dries to a thick crust, also unlike *Verdigellas*, which on drying, loses all thickness.

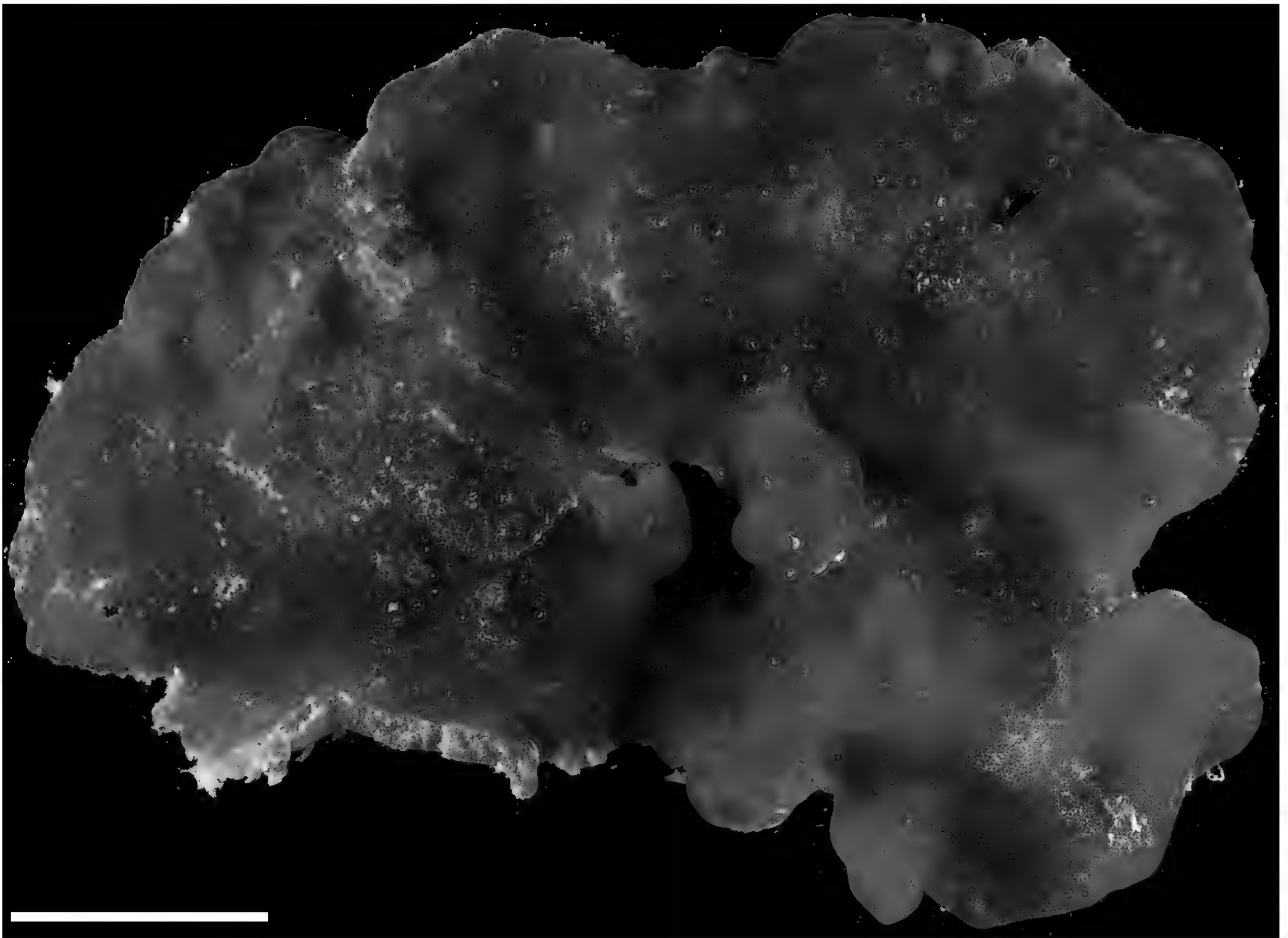


FIGURE 116. *Verdigellas peltata*. DLB8029: SE Mona Island, 70 m. Scale bar = 1.0 cm.





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# Glossary

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**D**efinitions provided in the International Code of Nomenclature (Turland et al. 2018) are appended in brackets, along with the corresponding article (Art.) number(s).

**acuminate** Tapering gradually to a point.

**aegagropiloid** An aggregation, frequently ball-like, of cells.

**akinete** Thick-walled, nonmotile, asexual resting spore.

**amyloplast** Organelles that produce and store starch.

**annulate** Possessing ringlike bands.

**apiculus** A small (sharp) point or tip; an alga possessing an apiculus is apiculate.

**aplanospore** Nonmotile asexual cell.

**aseptate** Without cross walls.

**asexual** Nongametic reproduction.

**assimilator** The upward-growing axis in *Caulerpa* species.

**auriculate** Ear shaped.

**basionym** The original name on which a species is based. [The legitimate, previously published name on which a new combination or name at new rank is based. The basionym does not itself have a basionym; it provides the final epithet, name, or stem of the new combination or name at new rank (Art. 6.10).]

**caespitose** Tufted.

**capitulum** A cluster with a head-like appearance.

**centripetal** Development toward the center.

**cervicorn** As in branching, in a manner similar to antlers of a deer.

**circumscription** The definition of taxonomic limits, including indication of the elements (e.g., subordinate taxa, synonyms, specimens, illustrations) that are included in a taxon.

**clavate** Club shaped.

**cleft** Partially divided.

**coccoid** Resembling small spheres.

**coenocytic** A single cell with multiple nuclei.

**concrecent** Growing together, to coalesce.

**congeneric** Belonging to the same genus.

**cordate** Heart shaped, with the indentation being lowermost.

**cortex** Outer layer of cells that have chloroplasts, normally cells to the exterior of the medulla.

**corticating** Referring to the cells or filaments that comprise the cortex.

**cortication** Tissue that overlies the medulla.

**crenate** With a scalloped or notched margin.

**crisate** Irregularly curled or crinkled.

**crustose** Possessing a thallus (sometimes thin) that adheres closely to the substrata.

**cuneate** Wedge shaped (=cuneiform).

**cyathiform** Funnel shaped.

**deciduous** Falling off.

**decumbent** Horizontal growth along the substratum; growing in a prone manner, not upright.

**deltoid** Delta shaped.

**dentate** Toothed.

**desmid** Group of freshwater algae, frequently with elaborate symmetrical shapes.

**determinate** Of limited growth potential.

**dichotomous** In reference to branching, with two equal branches.

**digitate** Fingerlike.

**dimorphic** Having two forms.

**disc** A plate or a ring of structures.

**distal** Toward the apex of a thallus or structure, opposite of proximal.

**distichous** Arranged in two opposite rows.

**dorsal** Upper surface.

**emarginate** With a shallow notch at the tip.

**endolithic** Growing within hard substratum.

**epiphyte** A plant attached to and growing directly on top of another plant.

**epithet** The genus or species name.

**epitype** Specimen designated in addition to the holotype specimen for purposes of clarification. [A specimen or illustration selected to serve as an interpretative type when the holotype, lectotype, or previously designated neotype, or all original material associated with a validly published name, cannot be identified for the purpose of the precise application of the name to a taxon (Art. 9.9).]

**ex** In nomenclature, notation indicating that the author(s) following the *ex* are proposing a new taxon name and giving credit for its recognition to another individual(s) who precedes the *ex*. The taxon name was either previously invalidly published or never published (e.g., the taxon name may be written on herbarium specimens or in notebooks, communicated in letters, or otherwise suggested).

**falcate** Hooked, curved like a sickle.

**filiform** Slender and cylindrical.

**flabellum** Fan-shaped blade (pl. flabella).

**flexuous** Bent in different directions.

**foliaceous** Resembling a leaf.

**furcate** Forked.

**gametangia** Structures in which gametes are formed.

**gametophyte** Haploid phase in species with an alternation of generations. Typically, the generation that produces male or female gametes.

**generitype** The type species of a genus.

**heteromorphic** Having multiple morphological expressions.

**heterotypic** [A name based on a type different from that of another name referring to the same taxon (Art. 14.4).]

**hexagonal** Six-sided shape with equal-length sides.

**holocarpic** A type of reproduction in which the entire cytoplasm is converted to gametes. Holocarpic reproduction is occasionally seen in some Bryopsidales genera.

**holotype** The one specimen or illustration indicated as the nomenclatural type by the author(s) of a name of a new species or infraspecific taxon.

**homotypic** [A name based on the same type as that of another name (Art. 14.4).]

**hyaline** Colorless.

**imbricate** Overlapping layers.

**in** In nomenclature where the preceding author published the name (in a different article).

**incised** With marginal slits or slices.

**isodiametric** Equal in length and height, squarish in shape.

**lacinate** Deeply divided into segments.

**lanceolate** Elongate, tapering distally.

**lectotype** One specimen or illustration designated from the original material as the nomenclatural type (in conformity with Art. 9.12) if the name was published without a holotype, if the holotype is lost or destroyed, or if a type is found to belong to more than one taxon (Art. 9.3).

**lentiform** Convex on both sides, bulging outward.

**leucoplast** An organelle that functions in starch storage.

**medulla** Internal tissue.

**mesophotic** Low-light, deeper-water (roughly defined as deeper than 30–40 m) habitats that support photosynthesis.

**moniliform** Bead-like.

**monosiphonous** Comprising a single siphon.

**monostromatic** A single layer.

**monotypic** A taxonomic group that contains only one subordinate taxon (such as *Blastophysa*).

**mucronate** Terminating in a short, sharp point.

**neotype** A specimen chosen to be the type specimen when original type material is lost. [A specimen or illustration selected to serve as nomenclatural type if no original material is extant or as long as it is missing (Art. 9.8, 9.13).]

**node** The point at which adjacent cells or segments intersect.

**nominate** In situations where a species is divided into subspecific taxa, the originally named species is referred to as the nominate taxon.

**oblate** Circular, but flattened at the poles.

**oblong** Elliptical in shape with blunt ends.

**obovate** Egg shaped, attached at narrower end.

**obtuse** Having a blunt or rounded end.

**orbicular** Flattened and circular.

**parenchymatous** Similar to tissue, formed by cells in close proximity.

**parietal** Internal and positioned against the periphery.

**pectinate** Resembling the arrangement of teeth of a comb.

**pedicel** A stalk, normally comprising one or few cells.

**peltate** Shield shaped and typically borne by a more or less centrally placed stalk.

**pendant** Hanging.

**perfoliate** Wherein a stipe continues growing through a blade.

**pinnate** Branches arranged on opposite sides of a common axis.

**plumose** Having a feathery appearance.

**polychotomous** Division into multiple branches.

**polyhedral** With reference to a geometric solid having many faces.

**proliferous** Producing an abundance of branches, not always from the expected area.

**protoplast** Cell protoplasm without a cell wall.

**proximal** Toward the base of a thallus or structure, opposite of distal.

**pubescent** Covered with short cells.

**pyrenoid** Structure within some chloroplasts; site of starch synthesis.

**reniform** Kidney shaped.

**reticulum** A network, formed by anastomosing cells of filaments.

**rhizoid** Attachment, absorptive or corticating filament.

**rhizome** Horizontally growing axis; in *Caulerpa*, the rhizome is frequently beneath the sediment surface.

**rhombic** Four sided, where sides are the same length.

**segregative** A form of cell division in Chlorophyta in which the protoplast divides into several multinucleate daughter protoplasts that form walls.

**sensu stricto** In a narrow or strict sense.

**septate** Partitioned.

**serrate** Marginally toothed.

**sessile** Attached without a stalk.

**simple** Not rebranched.

**siphonous** Referring to a coenocytic condition.

**spathulate** Spoon shaped, broader terminally and narrower toward the base.

**Spindle** Shape resulting from a terete object that tapers at both ends.

**sporophyte** Diploid phase in species with an alternation of generations.

**stipe** Stalk.

**sub** (1) A prefix, indicating nearly or almost; (2) beneath.

**suprabasal** With respect to cells in a filament, the suprabasal cell is the cell immediately above the basal cell.

**tentacula** Cells that possess small processes that provide attachment to adjacent cells. Literally meaning resembling tentacles.

**terete** Cylindrical.

**tortuous** Intricately and irregularly twisted.

**torulose** Cylindrical structure that is swollen and constricted at intervals.

**trabeculae** Internal slender strands of cell wall material.

**truncate** Possessing an abrupt transverse end.

**turbinate** Inversely conically shaped.

**type locality** The geographical location where the specimen that serves as the holotype was collected.

**type species** See holotype.

**undulate** Wavelike pattern in the margin of a frond.

**unistratose** One layer.

**utricle** Saclike in shape.

**vein** A defined line, usually made up of larger cells and seen on flattened blades.

**ventral** Lower surface.

**vesicle** Bladder-like structure.

**whorl** An arrangement of structures originating from a single point that surround an axis.

**zoidangia** Plurilocular sporangia that produce motile zoospores.

**zonate** Demonstrating banding.





# Index of Scientific Names

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**N**ames of Chlorophyta and Prasinodermatophyta taxa recognized in Puerto Rico are shown in **bold** type. Non-green alga taxa, synonyms, or taxa with a distribution outside of Puerto Rico are in nonbold type. Page numbers in **bold** type refer to account headings; page numbers in *italic* type refer to illustrations; page numbers in plain, nonitalic type refer to taxa mentioned in the text.

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